THESIS

SPECIES RICHNESS, DENSITIES, HABITAT RELATIONSHIPS, AND CONSERVATION OF THE AVIAN COMMUNITY OF THE HIGH-ALTITUDE FORESTS OF TOTONICAPÁN, GUATEMALA

Submitted by

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WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY KATHERINE ARDEN CLEARY ENTITLED SPECIES RICHNESS, DENSITIES, HABITAT RELATIONSHIPS, AND CONSERVATION OF THE HIGH-ALTITUDE FORESTS OF TOTONICAPAN, GUATEMALA BE ACCEPTED AS FULFULLING IN PART THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

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ABSTRACT OF THESIS

SPECIES RICHNESS, DENSITIES, HABITAT RELATIONSHIPS, AND CONSERVATION OF THE AVIAN COMMUNITY OF THE HIGH-ALTITUDE FORESTS OF TOTONICAPÁN, GUATEMALA

The Northern Central American Highlands, which include the mountains of Chiapas, Guatemala, El Salvador, and Honduras, are a recognized endemic bird area (Stattersfield et al. 1998) as well as a biodiversity "hotspot" (Myers et al. 2000). The coniferous forests of the regional park "Los Altos de San Miguel Totonicapán" lie within this region. Despite the importance of this area for global avian biodiversity, little research has been conducted in Los Altos, in part because the local Mayan authorities who manage the forest prohibit entry of all outsiders. As part of my Peace Corps Masters International work, I lived for 2½ years in the town of Totonicapán and gained entry to the forests of Los Altos. I worked with local community agencies to design a research project that provides both valuable baseline information on avian community composition, distribution, and abundance, and also a set of environmental education materials and income generation opportunities to help local communities achieve bird conservation. During the rainy and dry seasons in 2008-2009, we used standard distance sampling methods to conduct point counts at 34 locations in the forest. To explore patterns of bird habitat use, we measured 13 vegetation covariates at each point. Community-level analyses with program COMDYN indicated a high level of species richness which did not fluctuate between seasons, and canonical correlation analysis at the community

level revealed that average diameter at breast height of trees and understory density were relatively strong predictors of bird community composition. Species-level analysis of selected species revealed interesting patterns of detection probabilities and densities varying between seasons. Finally, species-habitat relationships were explored using an AIC framework and a model-averaging approach to determine the relative importance of vegetation covariates in predicting point level density of selected species. Results from this study reveal the previously unknown composition, distribution, and habitat use patterns of the avian community, and provide the Totonicapán Forestry Office, CONAP (Guatemalan National Park Service), and the local Maya K'iche' authorities with the first baseline information on avian ecology in the forests of Los Altos.

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throughout my life have been my most loyal fans; each achievement I have, no matter how small, is met with happiness and pride. I want to especially thank my parents and my two brothers for coming to visit me during my time in Guatemala.

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INTRODUCTION

Patterns of worldwide avian species composition and distribution have been investigated for many decades, yet ecologists' understanding of these patterns and the underlying processes which create them remain incomplete. Early studies of bird communities attempted to estimate the relationship between species diversity and habitat, specifically vegetation structure and composition (MacArthur and MacArthur 1961; MacArthur et al. 1966; Recher 1969; Karr and Roth 1971), and were mostly conducted in temperate regions of North American and Europe. More recently, researchers have begun to focus on the tropics, which support a large percentage of total global species as well as provide habitat for temperate-breeding migrants. Despite extensive work, large areas of the Neotropics remain unstudied (Terborgh et al. 1990; Levey and Stiles 1992; Petit and Petit 2003; Eisermann and Schultz 2005). Broadly, this study focused on partially filling that gap by 1) documenting the diversity and community composition of the avifauna of a unique Neotropical ecosystem, 2) estimating densities of bird species, particularly endemic and endangered species, and 3) investigating relationships between these species and their habitat.

Conservation context

The Northern Central American Highlands, which includes the mountains of Chiapas, Guatemala, El Salvador, and Honduras, are a recognized endemic bird area (Stattersfield et al. 1998) as well as a biodiversity "hotspot" (Myers et al. 2000). The coniferous forests of the

regional park “Los Altos de San Miguel Totonicapán” (Los Altos) lie within this region. Park lands are jointly managed by the Guatemalan National Park Service (CONAP), the municipal Forestry Office of the city of Totonicapán, and the local Maya K’iche’ authorities (CONAP 1997). Due to lack of information and funds and ongoing conflicts over management priorities and land ownership, none of these agencies has a master plan for the area and there is limited active management. Of the three agencies, the Maya K’iche’ authorities, the Alcaldes Comunales de los 48 Cantones (hereafter referred to as the Mayan Mayors Council) have the most power over forest management. CONAP is crippled by lack of funding and is only able to send personnel to Los Altos during the Christmas season, when urban demand for the decorative fir tree “el Pinabete” (*Abies guatmalensis*) causes widespread poaching of these endangered trees. The municipal Forestry Office maintains a large tree nursery on the southern edge of Los Altos and carries out several reforestation campaigns each year. However, aside from reforestation and sporadic environmental education programs, the Forestry Office is not deeply engaged in forest management. It is the Mayan Mayors Council that organizes annual forest mapping activities, gather feedback and commentary from the local people who depend of the forest, and control grazing and logging permits. The Mayan Mayors Council also strictly protects Los Altos from all external forces: no one from outside of the community of Totonicapán is welcome in the forest at any time.

Although the Maya K’iche’ people have extensive first-hand knowledge of the animals and plants which compose their forest, they do not have access to outside information about the global importance of these species or how to manage for their conservation. As a Peace Corps volunteer, I lived in the community of Totonicapán for almost three years, and gained

permission to work in Los Altos. With the approval of the Mayan Mayors Council, I designed and carried out the first formal study on the bird community of this unique forest. This work was possible because my degree is through the Peace Corps Masters International. As a student in this program, I completed course work at Colorado State University and subsequently traveled to Guatemala to live and work as a Peace Corps Volunteer for 31 months. During this time, it was also my responsibility to identify and implement my thesis research project.

In addition to my empirical research, I also used the results of this study to enrich and guide my projects as a Peace Corps volunteer. In collaboration with the Mayan Mayors Council and other local cooperators, I created a set of bird-related environmental education materials, organized and carried out two "Teaching Biodiversity" workshops with more than 100 teachers, published the first complete bird guide for Los Altos, established a bird-watching tourism project, and raised money for, planned, and carried out a two month guide-training to certify 15 local individuals as bird-watching guides. In the third chapter of this thesis, I detail some of the challenges and rewards of these collaborative conservation projects.

Conservation objectives

My principal conservation objective was to provide the local Maya K'iche' community with a better understanding of and appreciation for the diversity and fragility of the birds of their communal forest. The insights into the ecology of the bird community of Los Altos described here represent a valuable contribution to local knowledge and provide the three co-managing agencies with essential baseline information about how land use practices such as logging and grazing are affecting their avifauna. Additionally, it is my hope that this study provides future researchers with useful information about when and how to carry out ecological

studies in tropical ecosystems which claim management regimes as unique and surprising as their flora and fauna.

Ecological context

This is the first formal study focused on the ecology of the avian community in Los Altos de Totonicapán. The study builds off and extends existing, unpublished knowledge on birds in the Guatemalan highlands.

According to a preliminary list created using Howell and Webb (1995) and Peterson (1973, 1990), 140 resident bird species were expected to occur above 2500 m in the highlands of western Guatemala, at least 30 of which are regional endemics. Additionally, 58 migratory bird species were expected to utilize this area as part of their winter range (Howell and Webb 1995; Peterson 1990). A superficial inventory conducted by the Center for Conservation Studies (CECON) of the University of San Carlos Guatemala confirmed the occurrence of 33 resident and migratory bird species (Cano et al. 2001). In addition, a rapid assessment by CONAP researchers identified 32 species of resident and migrant birds (CONAP 2004). Clearly, more work was needed to collect baseline information about the avifauna of Los Altos.

In the first chapter of this thesis, I focused on community-level metrics. I reported the results of the complete inventory of the avifauna of Los Altos, and used ComDyn4 (U. S. Geological Survey, Pautuxent Wildlife Research Center) to estimate species richness in each season and community dynamics between seasons. I used canonical correlation analysis to reveal patterns between species richness and the vegetation structure and composition.

In the second chapter, I used program DISTANCE 6.0 (Thomas et al. 2009) to estimate global detection probability and density for five of the most common bird species in the study

area. Using these estimates, I calculated point-level densities and used regression models to estimate the relationship between bird density and the measured habitat covariates.

Ecological objectives

In this study, I had three principal ecological objectives: 1) to provide the first comprehensive baseline inventory of the bird community of Los Altos, 2) to estimate the community-level metrics of species richness and diversity, and to determine the relationship between these metrics and the patterns of habitat use, and 3) to estimate the species-level parameters of detection probability and density for the most commonly encountered species in the study area, and to relate these estimated densities to habitat covariates.

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CHAPTER 1: SPECIES RICHNESS AND HABITAT USE PATTERNS OF THE BIRD COMMUNITY

INTRODUCTION

"Reliable quantitative information on the structure and composition of tropical forest bird communities is scarce and sorely needed"

-Terborgh et al. 1990

Although this quote appeared in a paper published nearly 20 years ago, today there remain many areas of the tropics where little to no quantitative ecological information has been collected (Petit and Petit 2003; Eisermann and Schultz 2005). The high-altitude coniferous forest of the regional park of Los Altos de Totonicapán, Guatemala is one of those areas. Los Altos represents a unique and little-known ecosystem; it is one of the highest-altitude forests in Central America, and one of the largest contiguous forested areas in Guatemala, outside of the Petén (Albacete and Espinoza 2002). As is the case with many parks in the tropics, Los Altos is faced with intensifying human pressures on the forest, including logging, grazing, fire, and an advancing agricultural frontier. In order to adapt to these pressures and successfully protect the park's unique biodiversity, local forest managers urgently need basic ecological information

about the current status of bird populations within the park. This study helps provide that information.

Specifically, in this chapter I report valuable community-level information about bird species richness and diversity, and the relationship between these parameters and habitat in the forest. I used COMDYN to estimate species richness in each season and associated measures of spatial and temporal variation in bird species richness. I applied canonical correlation analysis to point-level species richness and habitat measurements in each season to explore dominant patterns of habitat use by the bird community of Los Altos.

Inventory of the avian community

According to the original land title, the forests of Los Altos belong to "the people of the community of Totonicapán" (Conz 2008). A centuries-old community organization, the Mayan Mayors Council is charged with managing and protecting the forests. Their management activities include annual mapping of forest boundaries, control of grazing and logging permissions, sporadic reforestation projects, and forest monitoring conducted by two part-time forest guards. Due to traumatic events during the Guatemalan Conflict (1966-1996), the Mayan Mayors Council is very wary of outsiders to the community, and does not allow anyone who is not a community member to enter the forest. This policy is enforced by the forest guards as well as by local people from communities surrounding the forests, who are constantly in the forest cutting down trees for firewood, grazing their livestock, or collecting moss, mushrooms, or other valuable forest products.

As a result of this protective attitude, very little scientific research has been conducted in the area, and virtually nothing of this unique ecosystem is known to the greater scientific

community. Universities, NGOs, and other organizations, which are often the primary source and support of researchers in the tropics, have not been able to enter Los Altos. The only published information about the park's biological resources consists of overall "state of the park" analyses by environmental non-profits (Albacete and Espinoza 2002; Probosques 2003), a superficial flora and fauna inventory by CONAP (2004), a rapid biodiversity assessment by researchers from the University of San Carlos (Cano et al. 2001), and a single, decades-old peer-reviewed publication on forest composition (Veblen 1978).

Clearly, there is a paucity of knowledge about the biological resources of this unique ecosystem. Generating this information is not only important to the larger scientific community, but also to the co-managing agencies and the local people who are the communal owners of the forest. During my time as a Peace Corps Volunteer, the Mayan Mayors Council expressed their desire to obtain information such as inventories of flora and fauna and management suggestions for problems like the pine beetle (*Dendroctonus* spp.) outbreak. Working together, we decided that the best application of my expertise and trusted position in the community was to conduct a study on the bird communities of Los Altos. Birds were chosen as a research focus because the majority of the fauna in Los Altos have been hunted out, leaving birds as one of the only remaining taxa with any significant level of abundance. In addition, birds provide a wide range of ecosystem services in tropical forests, and a diverse, abundant bird community is necessary to maintain a healthy forest ecosystem (Sekercioglu 2006). Given these considerations, a complete species inventory was a clear priority for this study.

Species richness

An inventory gives only the most basic information about the bird community of Los Altos. In order to further characterize bird community composition, I estimated species richness for my study area in each season. I applied the most recent estimation techniques, which allowed for heterogeneity in detection probability among species. Although increasing attention has been focused on the need to use sampling and analytic methods that account for this heterogeneity when estimating species richness and diversity (e.g., Buckland et al. 2001; Rosenstock et al. 2002; Buckland et al. 2004; Gale et al. 2009), relatively few studies actually incorporate these methods. Instead, many studies at the community level make two mistakes in estimating species richness: they equate species richness with the number of species in a sample, and they identify the relative abundance of two species from the ratio of sample counts (e.g., Greenberg 1997; Gillespie and Walter 2001; Marsden and Symes 2008). The former assumes all species are detected, while the latter assumes all species are sampled with equal probability, assumptions which almost never hold true in the field (Williams et al. 2001).

Another consideration which is often neglected in studies of species richness and diversity in tropical forests is that of seasonality (Marsden and Symes 2008). Often, logistical considerations dictate that researchers in the tropics have only a few weeks or even a few days to collect data. Information collected over such a short time period cannot adequately represent differences in species richness, diversity, and composition caused by the presence of migrants, by breeding, and by other effects of season. This study addressed seasonal changes in Los Altos by collecting data over almost an entire year, with multiple surveys during the dry and rainy seasons.

Relationship between the bird community and habitat

One of the first studies to quantitatively examine the linkages between avian community composition and vegetative complexity was by MacArthur and MacArthur (1961), who found that forest structure is a more important determinant of bird species diversity than forest composition. Subsequent studies tested this relationship across a variety of habitats and ecosystems. While some researchers confirmed MacArthur and MacArthur's results (MacArthur et al. 1966; Recher 1969; Karr and Roth 1971; Terborgh 1977; Beedy 1981; Hino 1985), others disagreed (Lovejoy 1972; Willson 1974; Karr 1980; Erdelen 1984; Rotenberry 1985). The latter studies argued that although in the majority of habitats forest structure may be correlated with bird species diversity, this explanation is largely phenomenological and probably masks responses to more specific determinants such as floristic composition, presence of other taxa, resource productivity, and changing trophic organization.

Clearly, assuming that the composition and distribution of the bird community is dependent on a single habitat measurement is imprudent. In all likelihood, individual organisms are not measuring single characteristics of the habitat, but are integrating myriad characteristics. Considering this, many researchers have chosen to measure a range of habitat covariates encompassing both structural and floristic characteristics, and then compare the results to determine which is more strongly correlated with species richness and diversity (Hino 1985; Rotenberry 1985; DeGraaf et al. 1998; Rotenberg 2007). In this study, I followed this integrative approach. I measured 12 habitat covariates which I judged to be important to the bird community of Los Altos, and then explored the relationship between these covariates and the composition of the bird community. There are many techniques available for examining the

relationships between sets of ecological data with multiple variables. When the primary goal of a study is to determine how species respond to particular sets of observed environmental variables, as in this study, the appropriate technique is canonical correlation analysis (CANCOR) (McGarigal et al. 2000).

Objectives

My objectives in this chapter were (1) to estimate species richness and associated measures of variation in species richness between seasons, and (2) to relate species richness to habitat characteristics using canonical correlation analysis. Insights derived from these analyses will provide a baseline for future monitoring efforts in Los Altos and will indicate which habitat characteristics should be preserved in order to maintain current levels of species richness .

STUDY AREA

Data were collected in the regional community park Los Altos de San Miguel Totonicapán, which lies in the department of Totonicapán in the western highlands of Guatemala (Figure 1). The park encompasses 16,404 hectares and is between the coordinates of 14º 49´/91º 11´ and 14º 56´/ 91º 19´, at elevations between 2,400 m and 3,403 m.

The vegetation complexes in the park include coniferous forests, mixed coniferous-broadleaf forests, brushlands, and high grasslands. The coniferous forests occur above 2,900 m and consist mainly of Ayacahuite pine (*Pinus ayacahuite*), the endemic Guatemalan Fir (*Abies guatemaltensis),* Endlicher pine *(Pinus rudis),* and smooth-barked Mexican pine (*Pinus pseudostrobus)*. The understory is composed of species from the Rosaceae and Lamiaceae families, and ferns (Veblen 1978; Albacete and Espinoza 2002). Mixed broadleaf-coniferous forests are found primarily below 2,900 m, and are dominated by oaks (*Quercus* sp.), Endlicher

pines (*Pinus rudis*), ocote pine (*Pinus oocarpa*), smooth-barked Mexican pine (*Pinus pseudostrobus*), rough-barked Mexican pine (*Pinus montezumae*), Ayacahuite pine (*Pinus ayacahuite),* and Cypress (*Cupresuss lusitanica).* The understory of these forests includes Alders (*Alnus spp.*), Texas madrone (*Arbutus xalapensis*) and prickly heath (*Pernettya mucronata*) (Veblen 1978; Albacete and Espinoza 2002). Natural brushlands occur above 2,500 m, and are composed of *Baccharis spp., Buddleia nitida, Acaena elongate,* and *Pernettya ciliate* (Veblen 1978). Occasional high-altitude meadows are found above 2,800 m.

The study area was composed of a plot of approximately 200 hectares, located on the western edge of Los Altos (Figure 1). Since the purpose of this study was to determine composition and distribution of forest birds, points were restricted to the coniferous and mixed coniferous-broadleaf habitat types.

METHODS

Bird survey data

Data were collected using the variable circular plot method (Reynolds et al. 1980; Buckland et al. 2001), hereafter referred to as point counts. Thirty-four points were placed at random across an elevational gradient (2700-3300m) in the 200 hectares study area. Since the purpose of this study was to determine composition and distribution of forest birds, points were restricted to the coniferous and mixed coniferous-broadleaf habitat types. All points were surveyed twice during the rainy season (in April-May 2009) and four times during the dry season (in December 2008-February 2009). Each point was surveyed for 10 minutes from 0600 – 0930, therefore, nocturnal birds are not included in these analyses. All birds detected within 25 m and the horizontal distance from the point to the bird were recorded. Horizontal distance detection

was standardized by marking distances with survey tape on the first visit to the point. Individuals flying over the point were not counted. These detections, as well as individuals detected outside of the 25 m radius or detected while traveling between points, were recorded as incidental detections and were used in calculations of global species richness and diversity.

Vegetation data

A modified James-Shugart method was used to measure habitat variables at each point (James and Shugart 1970; Noon 1981). A circle of radius 11.2 m was centered at the point, and within that circle the following vegetation characteristics were measured: 1) number of stems >1inch in diameter, 2) number of individuals of each tree species present, 3) DBH of all stems >1inch in diameter, 4) understory foliage density (using density board as per Noon 1981), 5) number of shrub species present, 6) percent canopy closure (calculated along transects as per Noon 1981), 7) average canopy height, and 8) average understory height (Noon 1981; Renner et al. 2006; Smith 2008).

These measurements yielded the following vegetation variables: 1) total tree density (stems/hectares), 2) tree species richness, 3) dominant tree species, 4) average DBH across all trees, 5) percent canopy closure, 6) average canopy height, 7) understory foliage volume at four heights, 8) shrub species richness , and 9) average understory height. Tree species richness, dominant tree species, and shrub species richness are floristic variables chosen to reveal habitat associations of bird species and communities, whereas total tree density, average DBH, understory foliage volume, canopy closure, and average canopy and understory height are structural variables that can serve as simple indices of disturbance (Rotenberry 1985).

Species richness

I used program COMDYN4 to estimate species richness and associated variation in related measures of community dynamics over time using the online interactive COMDYN software (Hines et al. 1999). COMDYN is based on the Jackknife estimator, which calculates the variability of a statistic from the variability of that statistic between subsamples, rather than from parametric assumptions (Williams et al. 2002). The advantage of this estimator over traditional parametric estimators is that it is robust to variation in detection probabilities among species, whereas parametric estimators are negatively biased in this situation (Burnham and Overton 1979).

I grouped the point count data by season so that COMDYN estimated species richness separately in each season. With this data structure, I was also able to use COMDYN to compare proportions of shared species between seasons, estimate the number of species present in one season but not the other, compute "extinction" and "colonization" probabilities, and calculate average species detection probability by season (Table 4).

Relationship between the bird community and habitat

CANCOR is a multivariate statistical technique which allows finding the axes that maximize the linear correlation between two sets of variables – in this study, a group of species representing the bird community and habitat characteristics (McCune 1999). In CANCOR, data sets with many variables and small sample sizes can be difficult to interpret and may give spurious results, because as the number of variables approaches the sample size, the canonical correlation will always approach one. One rule of thumb is that the sample size should be three times larger than the sum of the variables in each set (McGarigal et al. 2000). In this study, a

total of 12 vegetation covariates were measured at each of the 34 survey points, and 50 species were detected during point counts. This number of variables clearly violates the limitations of CANCOR.

To address this problem, I restricted the analysis to a subset of the habitat and species variables. I used scatterplot matrices and a correlation matrix in R (2.10.1) to check for collinearity in the habitat covariates. I eliminated one of each set of habitat covariates with a correlation coefficient >0.60 or with a correlation coefficient >0.40 with two or more other covariates (Table 2). Although unnecessary if the primary goal of a study is prediction, this step is essential when the primary goal is describing species-habitat relationships; in order to reveal species-habitat relationships, parameter estimates must be accurate, and multicollinearity of predictor variables may affect parameter estimation (Legendre and Legendre 1998). Using these criteria, I eliminated seven of the 12 original covariates: dominant tree species, tree density, average canopy height, understory volume at two heights, shrub species richness, and average understory height. I then created a new, combined understory covariate, which represents understory density at all four levels measured (from 0-3 m) and is hereafter referred to as "understory density."

The final four covariates used in subsequent CANCOR analyses were average dbh, percent canopy closure, tree species richness, and understory density. These covariates represent specific impacts on the forest or specific forest types. Average dbh and percent canopy closure reflect logging practices, as both of these covariates will generally have high values at points which have not been logged and low values at points where the mature trees have been logged. Tree species richness reflects the type of habitat at the point; points in mixed

broadleaf-coniferous forest will have higher values of this covariate than points in conifer forest. Finally, understory density reflects grazing practices; areas with high levels of livestock grazing will have low values of understory density, and the converse. These covariates comprise the habitat variable set.

To reduce the number of variables in the bird data, I first selected only the top five most commonly detected species across seasons: the Pink-headed warbler (*Ergaticus versicolor*), the Amethyst-throated hummingbird (*Lampornis amythestinus*), the Rufous-browed wren (*Troglodytes rufociliatus*), the Brown creeper (*Certhia americanus*), and Steller's Jay (*Cyanocitta stelleri*). I then added two additional species which were commonly detected in both seasons and which, with the other species, more accurately represent the entire bird community: the White-eared hummingbird (*Hylocharis leucotis*) and the Rufous-collared robin (*Turdus rufitorques*). The White-eared hummingbird was chosen because the Trochilidae family is the second most common family (9.6 percent of species are in this family) after Parulinae, which is already represented in the top five most detected species. The robin was chosen because the family Turdidae is the sixth most common family in the study area (7.4 percent of species are in this family), and is not represented in the top five most detected species. These seven species comprise the species variable set.

I prepared the data for analysis in CANCOR by creating a single data matrix containing the species and habitat variables. A separate matrix was created for the dry and rainy seasons. To create the species portion of each matrix, I used the average raw count for each bird species at each point (i.e. number of times bird was detected/number of surveys). The ideal parameter for this response matrix would be point-level densities corrected for detection probability.

However, the total number of detections for a given species at a given point was not high enough to reliably estimate this parameter. In this study, the use of uncorrected raw counts was justified by the high average species detection probability calculated in COMDYN. According to these estimates, the probability that a species was detected in the dry season was $\hat{p}$ = 0.93 (0.81, 1.00), and in the rainy season was $\hat{p}$ = 0.92 (0.83, 1.00). Since these detection probabilities approach one, the raw count is an acceptable proxy for actual abundance at the point level.

One of the assumptions of CANCOR is that the relationships between the predictor and response variables are linear. In order to test this assumption with my data, I created scatterplots of the raw count of all bird species detected at each point against each of the final four habitat covariates. I repeated this process separately for each season. None of the habitat covariates showed clear non-linear relationships with bird species richness.

I used the CCA package in R statistical software (2.10.1) to conduct my CANCOR analysis. I first examined the correlations within each set of variables to ensure that no collinearity problems remained. I then calculated three important parameters: the canonical correlations for each canonical variate, the structure coefficients for each variable with each canonical variate, and the redundancy coefficients for each canonical variate. The canonical correlations measure the strength of the correlation between corresponding canonical variates from each set of variables, and the canonical correlation squared is equal to the eigenvalue for that pair of variates (McGarigal 2000). While this metric is useful for evaluating the importance of each canonical variate, the relationship it describes is between the variates rather than the original variables, which limits its utility as an interpretive tool. The canonical correlations are still

essential, however, since they are used in the calculations of the final two metrics. Therefore, I computed these correlations and tested them for statistical significance using a Wilk's Lambda test (Canonical Correlation Analysis, UCLA, 2010). The final two metrics, structure coefficients and redundancy coefficients, are far more useful for interpretive purposes. They are both measures of *redundancy* (the amount of variance in the original variables of one set that can be explained by a given canonical variate from the other set), and as such are the most important piece of output from CANCOR (McGarigal 2000).

RESULTS

Inventory of the avian community

A total of 94 species were identified in the Los Altos inventory (Appendix 1). Of these species only 50 were detected during point counts. The remaining 44 species were either nocturnal and so not detected in morning counts (Strigidae, Tyrannidae), species which spend the majority of their time in flight and so were only documented passing over points (Cathartidae, Accipitridae, Apodidae, Hirundinidae), species which use mostly edge and agricultural habitat not included in the study area (Corvidae, Passeridae, Fringillidae, Icteridae), or were incidental detections identified between point counts.

Following Howell and Webb's (1995) definition of endemism, 27 of the 94 species (28.7 percent) detected were regional endemics. Additionally, 11 of the 94 species (11.7 percent) detected were Neotropical migrants (Appendix 1). Two species of global concern were detected in Los Altos: the vulnerable Pink-headed Warbler (*Ergaticus versicolor*) and the endangered Horned Guan (*Oreophasis derbianus*) (IUCN 2010).

Species richness

Analysis with COMDYN yielded an estimate of species richness of 48.56 (45.00, 55.69) for the dry season and 43.43 (40.00, 47.55) for the rainy season. Although species richness appeared to be marginally higher in the dry season than in the wet season, the difference was not significant (Figure 2). The proportion of species present in the dry season which were still present in the rainy season was $\Phi = 0.83$ (0.70, 0.98). Hines et al. (1999) derive an "extinction probability" using the formula $1-\Phi$; in this study the extinction probability was more appropriately interpreted as the probability of migration, which would be 1-0.83 = 0.17. Conversely, the proportion of species present in the rainy season which were also present in the dry season was 0.93 (0.69, 1.00). There were an estimated 3.14 (0.00, 10.62) species present in the rainy season which were not present in the dry season.

As described above, the estimated average detection probability for species approached one in both seasons. In the dry season, average detection probability for a given species was 0.93 (0.81, 1.00) and in the rainy season, average detection probability was 0.92 (0.83, 1.00).

Relationship between the bird community and habitat

The first canonical variate in the dry season is characterized by high average dbh (-0.8388) and high levels of understory density (-0.5054) (Table 4). Tests of dimensionality indicated that the first two of the four canonical variates were statistically significant ($\alpha<.05$) in the dry season. In the rainy season, the first canonical variate was dominated by tree species richness loading high on one end of the gradient (0.6650) and canopy closure on the other end (-0.6878). However, tests of dimensionality indicated that none of the variates were significant at the $\alpha = 0.05$ level in the rainy season (Table 5).

In the dry season, the significant first variate had a canonical correlation of 0.877, and the significant second variate had a canonical correlation of 0.671 (Table 4). In the rainy season, the non-significant first variate had a canonical correlation of 0.755, and the similarly non-significant second variate had a canonical correlation of 0.596 (Table 4). Note that a high canonical correlation alone does not guarantee a high level of redundancy between the canonical variates and the original variables – in the dry season, the first canonical variate explained 17.81 percent of the variation in the original species variables, and in the rainy season the first canonical variate explained only 11.02 percent of the variation in the original species variables (Table 4).

DISCUSSION

Inventory of the avian community

This inventory represents the first baseline information about the avian community of the forests of Los Altos. Previous partial species lists (Cano et al. 2001; CONAP 2004) listed only 33 bird species, whereas this inventory identified 94 species, including two species of global concern, the Pink-headed warbler (*E. versicolor*) and the Horned Guan (*O. derbianus*), whose presence in the forest increases the urgency for conservation of this critical habitat.

The Pink-headed Warbler is an endemic species with a very restricted range; in fact, the remaining habitat for the species is small enough to qualify it as endangered, but because there are recent records from more than five locations, the IUCN continues to rank it as vulnerable. This bright, active warbler is extremely abundant in the forests of Los Altos (see Chapter 2 of this thesis for density estimates). The endangered Horned Guan is also very range-restricted; it occurs only in the highlands of Chiapas and Guatemala, and in very fragmented populations

(IUCN 2010). This species was uncommon in Los Altos, occurring only in a few mixed-forest patches on the northwestern edge of the study area. Further work is needed to determine the local range and abundance of this species. There is a significant regional conservation project focused on the Horned Guan, and more information about its presence in Los Altos could help this park to be included in this project's plans (Center for the Conservation of the Horned Guan, 2010).

The inventory revealed a high level of endemism in the bird community of Los Altos. Nearly 29 percent of the species detected across the dry and rainy season are regional endemics, with a total range of less than 50,000 km^2 (BirdLife International; Howell and Webb 1995) (Appendix 1). This is not surprising, because the forests of Los Altos lie within the North Central American Highlands, where complex topography and high altitudes isolate ecosystems and favor speciation, thus leading to high levels of endemism across taxa (Breedlove and Heckard 1970; Stattersfield et al. 1998). Of the 20 endemic species which occur in this area and have earned it official designation as an important Endemic Bird Area, 10 occur in the forests of Los Altos (Horned guan (*Oreophasis derbianus*), Ocellated quail (*Cyrtonyx ocellatus*), Green-throated mountain gem (*Lampornis viridipallens*), Blue-throated motmot (*Aspatha gularis*), Black-capped swallow (*Notiochelidon pileata*), Blue-and-white mockingbird (*Melanotis hypoleucus*), Black-capped siskin (*Carduelis atriceps*), Rufous-collared robin, Rufous-browed wren, and Pink-headed warbler) (BirdLife International). The fact that Los Altos provides critical habitat for such a large number of endemic species lends new urgency to efforts to protect the park.

It is interesting to note that fewer migrants than expected were detected in the study area. This may be due to the fact that Los Altos has a perennially cool climate, with an average annual temperature of 9º C, which in the coldest months can drop to -7º C (Albacete and Espinoza 2002; Probosques 2003). Neotropical migrants leave the northern latitudes in search of warmer temperatures and more abundant resources. The cold climate and relatively poor plant diversity of the coniferous forests of Los Altos make it a less-than-ideal wintering range. In comparison, the lower-altitude, lush, complex cloud forests surrounding the nearby Lake Atitlan support a much more diverse and abundant community of Neotropical migrants during the dry season (CONAP 2004; K. Eisermann, personal communication).

Species richness

Since the dry season corresponds with the northern winter, during which Neotropical migrants are present in Los Altos, it is no surprise that estimates of species richness by season revealed that richness is slightly higher in the dry season than in the rainy season, although this difference is not significant (Figure 2). Another possible driver of this pattern is that the majority of trees and understory plants in Los Altos flower during the dry season, probably in order to maximize vegetative growth in the wet season and take advantage of pollinating and dispersing agents in the dry season (Heithaus et al. 1975; Veblen 1978; Lic.P. Pardo, personal communication). This attracts some altitudinal migrants from lower-altitude habitats which do not have such a defined dry and rainy season, and these local migrants also contribute to increased species richness in the dry season (Howell and Webb 1995; see also Chapter 2 of this thesis). The difference in species richness was not significant with this data set; however, given the ecological patterns I observed, I propose that additional data collection with more point

surveys in the rainy season may reveal a significant difference in species richness between seasons. If this were the case, then future researchers interested in studying complete bird communities in high-altitude tropical forests like Los Altos should plan their data collection for the dry season, when the entire complement of species is present.

It is important to note that the estimates of species richness calculated with COMDYN were far lower than the actual species richness observed through the inventory process. This is because of the 94 species identified in the inventory, only 46 were detected during point counts in the dry season, and only 41 were detected during point counts in the rainy season. The remainder of these 94 species was detected incidentally, while traveling between points or on leisure hikes in the forest. To improve these estimates, future studies should increase the number of point surveys and place additional points in different microhabitat types, such as humid, low-elevation gullies adjacent to streams.

In addition to species richness, COMDYN also calculates measures of variation in species richness between seasons. One of the most interesting of these is the local extinction probability parameter, 1-Φ. In studies where data were collected over various years, this parameter can be interpreted as the probability that a given species present in one year will go extinct by the next year (Hines et al. 1999). In this study, the dry and rainy seasons were too close together in time (December-February and May-June of 2009) to consider that 1-Φ realistically represents an extinction probability. Instead, I interpreted it as the probability that a species present in the dry season was not present in the rainy season: a migration probability. The estimated migration probability was thus $1-\Phi = 0.17$. This estimate makes intuitive sense, because 11.7 percent of the species detected in the study area were Neotropical migrants. The

remaining 5.3 percent of species which should migrate according to this estimate were probably altitudinal migrants which leave Los Altos when the abundant flowering of the dry season ends. COMDYN also estimates a second, related parameter, the number of colonizing species (β). I interpreted this parameter similarly to the extinction parameter 1-Φ; instead of colonizing species, β represents the number of species who used the study area during the rainy season, but moved to lower altitudes in search of different resources or to avoid cold temperatures of Los Altos during the dry season (Albacete and Espinoza 2002). This pattern of altitudinal migration has been noted in similar cold, high-altitude forests in Central America (Levey and Stiles 1992; Lara 2006).

Relationship between the bird community and habitat

Based on the results of the CANCOR analysis, two characteristics of the habitat in Los Altos had a relatively strong impact on the composition of the bird community, at least during the dry season. In this season, CANCOR results indicated that points with a higher average dbh and with denser understory had higher levels of species richness and abundance. Specifically, 17.81 percent of the variation in the composition of the seven species subset of the bird community was explained by the variation in the first habitat covariate, which was dominated by average dbh and understory.

These results broadly support the hypothesis that logging of large, mature trees and grazing down the understory of the forest have a significant impact on the bird community. Similar patterns have been found in other recent studies of bird-habitat relationships. These studies have shown that habitats affected by human disturbance generally offer lower vegetative complexity (due to fewer canopy and understory layers); accordingly these habitats

support lower levels of species richness and diversity (Hanowski et al. 1997; Thiollay 1997; Petit et al. 1999). In one review of more than 40 published papers comparing species richness/diversity in a variety of plant and animal taxa along a gradient of disturbance from primary forest to agro-ecosystems, the majority of the papers recognized a significant decrease in species richness and diversity from more pristine to completely agricultural landscapes (Scales and Marsden 2008). This intuitive pattern is supported by my analysis of bird-habitat relationships in the heavily impacted forests of Los Altos.

At this point, I cannot generalize from the CANCOR analysis to the entire bird community of Los Altos. As described in the Methods section, one of the limitations of CANCOR is that the sample size must be at least three times larger than the sum of the response and predictor variables. To meet this requirement, I had to limit my species data set to only seven of the more commonly detected species. Although I carefully selected species in an effort to represent the range of habitat requirements of the entire bird community, there is no possible way that seven species from six families could accurately represent the habitat requirements of all 50 species from 19 families detected during point surveys.

There are several other considerations which limit the inferences that can be drawn from this analysis. Since the highest redundancy coefficient for any significant variate in either season was only 17.81 percent, it is likely that there were other habitat characteristics not measured in this study which are significant determinants of bird community composition in Los Altos. Measuring these variables and including them in the habitat variable set of a new CANCOR analysis would change the formation of the canonical variates, and could completely change the interpretation of the results. Including additional or different species in the set

could have similar effects. As with many ecological studies, the most effective solution to these analysis problems is to have a larger sample size; more points in the forest, spread across a larger geographic area, would allow more bird species and more habitat characteristics to be included in the corresponding variable sets, which would allow for a more complete understanding of the relationship between the two.

Despite these limitations, this study reveals one indisputable truth: the forest of Los Altos provide critical habitat to a diverse bird community with high levels of endemism, and this habitat is threatened by current land-use practices, especially logging and grazing. Given that the population of Totonicapán is growing at an annual rate of 2.09 percent, human-generated pressures on forest resources will only intensify in coming decades (CIA World Fact Book, 2009). It is essential that local managers, especially the Mayan Mayors Council, have the baseline ecological information necessary to influence land use practices in a way that protects and rewards both the birds and the people who depend on this forest for survival.

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CHAPTER 2: ESTIMATES OF DETECTION PROBABILITIES, DENSITIES, AND HABITAT USE PATTERNS OF SELECTED SPECIES

INTRODUCTION

The high-altitude coniferous forests of Los Altos de Totonicapán, Guatemala represent a unique, threatened, and little-known ecosystem. Los Altos lies within the Northern Central American Highlands, which includes the mountains of Chiapas, Guatemala, El Salvador, and Honduras. This highland region contains several recognized important bird areas and is considered to be a global biodiversity "hotspot" (Stattersfield et al. 1998; BirdLife International; Myers et al. 2000). Los Altos is managed by local Maya K'iche' authorities, who are very protective of the forest and do not allow entry by outsiders; as a result, very little biological information has been collected from this forest, and even less has been published. This study represents the first formal research conducted on the bird community of Los Altos.

In this chapter I focus on estimating species-level metrics for five of the most commonly detected birds (hereafter referred to as "focus species") in the study area, which lies on the western edge of Los Altos. I used program DISTANCE 6.0 to estimate global detection probability and density for each species (Thomas et al. 2009). Using these estimates, I calculated point-level densities and applied an information theoretic approach using Akaike's Information Criteria corrected for small sample size (AICc) to model the point-level density estimates as a function of measured habitat covariates.

Estimates of detection probability and density

Knowledge of the density of animals in a landscape is a key variable for effective wildlife management, but is difficult to estimate. In early ecological studies, species density or abundance was calculated using raw count data without correcting for the probability of detection, a practice which leads to underestimation of abundance and incorrect inferences about species-habitat relationships (Reynolds et al. 1980; Buckland et al. 2001; Rosenstock et al. 2002; Gale et al. 2009). In fact, a review by Rosenstock et al. (2002) found that 95 percent of studies investigating bird abundance applied "index count" methods in which detection probability was improbably assumed to be equal among all study points, observers, time of day, and season.

The most appropriate alternative to index count methods is distance sampling. Although not widely used until recent decades, using distance sampling to correct abundance counts by detection probability was applied in field ecology as early as the 1930s (Buckland et al. 2001). The point count variation on line transect sampling, also called variable circular plot sampling, was not developed until the 1970s, and became more popular after the publication of a methods paper (Reynolds et al. 1980). Although point count sampling restricts observers to a smaller area than does line transect sampling, it has compensatory advantages. It allows the observer to be stationary and thus detect canopy birds and secretive birds more easily in a dense forest, and it allows the researcher to more accurately determine sampling effort and the correlations between habitat and bird densities (Reynolds et al. 1980). In short, point count sampling is an inexpensive and effective way to inventory and monitor avian species, especially

in the tropics where forests can be structurally complex and many birds are secretive and difficult to detect with line transect sampling (Jimenez et al. 2000; Gale et al. 2009).

In this study, I applied distance-sampling methods to collect data on the bird community of the forests of Los Altos. I made repeated visits to 34 points randomly placed across the 200 hectare study area, and obtained sufficient detections for five bird species to calculate global estimates of detection probability and density for each species.

Habitat use patterns

Identifying relationships between birds and the structural and floristic components of their habitat is essential for determining how different land use regimes may affect overall composition of the avian community and status of species of special concern. To identify patterns in avian habitat use in Los Altos, I measured a set of habitat covariates at each point and modeled the relationship between these covariates and point-level densities of each of the five focus species.

One common and potentially problematic phenomenon in ecological data is the presence of spatial autocorrelation in the response variable. Spatial autocorrelation (SAC) refers to the fact that points close together in space are often more similar than points far apart in space; if SAC is unaddressed in ecological data, the Type I error rate increases (i.e. falsely rejecting the null hypothesis), leading to unreliable parameter estimates. Among the most common procedures used by ecologists to test for the presence of SAC in their data are Moran's I and Geary's c (Legendre and Legendre 1993; Fortin and Dale 2002; Dormann et al. 2007). These coefficients measure the similarity between values (e.g., density) at points as a function of the distance between the points. If significant spatial autocorrelation is detected in ecological data,

a special modeling approach which explicitly models spatial autocorrelation effects should be applied. This type of approach allows investigators to explain not only the amount of variation in point-level species density explained by the habitat variables, but also the amount of variation explained explicitly by the spatial variation in these habitat variables (Lichstein et al. 2002). Since my study area in the communal forest was limited in size (200 hectares) but contained diverse habitat types, I expected to find SAC in the point-level density estimates.

Objectives

My objectives in this chapter were 1) to estimate global detection probability and density for the most commonly detected species in the study area, and 2) to model point-level density estimates for each species as a function of measured habitat covariates. This modeling process yielded an initial idea of which habitat characteristics were relatively most important to support high densities of the focus species.

STUDY AREA

Data were collected in the regional community park Los Altos de San Miguel Totonicapán, which lies in the department of Totonicapán in the western highlands of Guatemala (Figure 1).

The vegetation complexes in the park include coniferous forests, mixed coniferous-broadleaf forests, brushlands, and high grasslands. The coniferous forests occur above 2,900m and consist mainly of Ayacahuite pine (*Pinus ayacahuite*), the endemic Guatemalan Fir (*Abies guatemaltensis),* Endlicher pine *(Pinus rudis),* and smooth-barked Mexican pine (*Pinus pseudostrobus).* The understory is composed of species from the Rosaceae and Lamiaceae families, and ferns (Veblen 1978, Albacete and Espinoza 2002). Mixed broadleaf-coniferous

forests are found primarily below 2,900 m, and are dominated by oaks (*Quercus* spp.), Endlicher pines (*Pinus rudis*), ocote pine (*Pinus oocarpa*), smooth-barked Mexican pine (*Pinus pseudostrobus*), rough-barked Mexican pine (*Pinus montezumae*), Ayacahuite pine (*Pinus ayacahuite),* and Cypress (*Cupresuss lusitanica).* The understory of these forests includes Alders (*Alnus spp.*), Texas madrone (*Arbutus xalapensis*) and prickly heath (*Pernettya mucronata*) (Veblen 1978; Albacete and Espinoza 2002). Natural brushlands occur above 2,500 m, and are composed of *Baccharis spp., Buddleia nitida, Acaena elongate, and Pernettya ciliate* (Veblen 1978). Occasional high-altitude meadows are found above 2,800 m. The study area was composed of a plot of approximately 200 hectares, located on the western edge of Los Altos (Figure 1).

METHODS

Bird survey data

Data were collected using the variable circular plot method (Reynolds et al. 1980; Buckland et al. 2001), hereafter referred to as point counts. Thirty-four points were placed at random across an elevational gradient (2700-3300 m) in the 200 hectares study area. Since the purpose of this study was to determine composition and distribution of forest birds, points were restricted to the coniferous and mixed coniferous-broadleaf habitat types. All points were surveyed twice during the rainy season (in April-May 2009) and four times during the dry season (in December 2008-February 2009). Each point was surveyed for 10 minutes from 0600 – 0930, therefore, nocturnal birds are not included in these analyses. All birds detected within 25 m were recorded, and the horizontal distance from the point to the bird was also recorded. Horizontal distance detection was standardized by marking distances with survey tape on the

first visit to the point. I did not count individuals flying over the point. These detections, as well as individuals detected outside of the 25 m radius or detected while traveling between points, were recorded as incidental detections and were used in calculations of global species richness and diversity.

Vegetation data

A modified James-Shugart 1970 method was used to measure habitat variables at each point (James and Shugart 1970; Noon 1981). A circle of radius 11.2 m was centered at the point, and within that circle I measured the following vegetation characteristics: 1) number of stems > 1 inch in diameter, 2) number of individuals of each tree species present, 3) DBH of all stems > 1 inch in diameter, (cm) 4) understory foliage volume (using density board as per Noon 1981, %), 5) number of shrub species present, 6) percent canopy closure (calculated along transects as per Noon 1981), 7) average canopy height, and 8)average understory height (Noon 1981; Renner et al. 2006; Smith 2008).

These measurements yielded the following vegetation variables: 1) total tree density (stems/hectare), 2)tree species richness, 3) dominant tree species, 4) average DBH across all trees, 5) percent canopy closure, 6) average canopy height, 7) understory foliage volume at four heights, 8) shrub species richness , and 9) average understory height. Tree species richness, dominant tree species, and shrub species richness are floristic variables chosen to reveal habitat associations of bird species and communities, while the variables of total tree density, average DBH, understory foliage volume, canopy closure, and average canopy and understory height are structural variables that can serve as simple indices of disturbance (Rotenberry 1985).

Estimates of detection probability and density

Estimates of detection probability ($\hat{P}$) and density ($\hat{D}$) were calculated for species with more than the minimum recommended detections (>30 in each season), using program DISTANCE, Version 6.0 (Thomas et al. 2009). Five species met these criteria: the Pink-headed warbler (*Ergaticus versicolor*), the Amethyst-throated hummingbird (*Lampornis amethystinus*), the Rufous-browed wren (*Troglodytes rufociliatus*), the Brown creeper (*Certhia americanus*), and the Steller's Jay (*Cyanocitta stelleri*). To obtain a detection probability for hummingbirds, one of the most common families of birds in the study area, detections for species with similar vocalizations were pooled to obtain an adequate sample size. This dataset contains pooled detections from the Broad-tailed hummingbird (*S.p.platycerus*), Magnificent hummingbird (*E.fulgens*), White-eared hummingbird (*B.l.leucotis*), and Azure-crowned hummingbird (*A.c.cyanocephala*). This dataset is hereafter referred to as Pooled Trochilidae.

For each of these six variable-distance data sets, I conducted an exploratory data analysis in Excel to choose a set of candidate models for the detection function. In all models, distance bins were defined to counteract the effects of heaping in the observations, and observations were right-truncated at the effective radius indicated by initial analysis. Three models were considered for each data set: half-normal, hazard-rate, and multiple models where the half-normal and hazard-rate curves could be fit separately by season. Although models used in DISTANCE 6.0 are robust to changes in detection probability, stratifying by season improves precision and reduces bias of estimates (Rosenstock 2002). Stratification improves density estimates because ecological differences between seasons such as weather, plant phenologic stages, and bird life cycle stages are likely to affect detection probability and/or density of some

species. Accordingly, I post-stratified by season (dry and rainy) for all models; all of the data sets had a minimum of 30 detections in each season. The survey effort at each sampling point was the total number of visits to that point in each season. Since the survey effort was not great enough to calculate point-level detection probabilities and density estimates, I calculated these parameters at the global level for each species. From the final model set for each species, I selected a best model based on AICc, and whether or not the model fit biological expectations. This modeling process is summarized in Figure 3.

Habitat use patterns

Several preliminary steps were necessary before modeling the relationship between densities of the focus species and habitat covariates. First, the density estimates were global estimates, based on pooled detection histories across all points; modeling of habitat use patterns based on vegetation covariates measured at the point scale required point-level density estimates. These were calculated for each of the focus species, separately for each season, using global detection probability. The formula for point level density is as follows:

$$D_i = c_i / \hat{p}_{i\text{global rainy or global dry}}$$

where c_i is the raw count of detections for that species made at point *i*. Geographic coordinates (UTMs) were then added to each point. Density was not estimated for the pooled hummingbirds, since a density estimate for pooled species assumes equal detectibility. Therefore, that data set was not included in these calculations or in the subsequent modeling process.

A second preliminary step was to test for spatial autocorrelation in the point-level density estimates. Since my study area contained diverse habitat types as a result of varying

levels of human disturbance and microhabitats created by humid valleys where deciduous rather than coniferous vegetation predominated, it was possible that density of bird species would display SAC, or that point proximity would affect density estimates (Dormann et al. 2007). I tested for SAC in the point level density estimates for each of the five species, separately by season. After confirming that SAC was not significant in any of the focus species, I fit general linear regression models and applied an information theoretic approach using AICc to model point-level estimates of species densities as a function of habitat covariates.

A third preliminary analysis step was reducing the number of habitat variables. Since a total of 12 habitat covariates were measured and the number of points was low (n = 34), I restricted the analysis to a subset of these covariates (Burnham and Anderson 2002). I used scatterplot matrices and a correlation matrix (R statistical software package 2.10.1) to test for high collinearity in the covariates. I eliminated one of each set of covariates with a correlation coefficient >0.60 or with a correlation coefficient >0.40 with two or more other covariates (Table 2). This step is not necessary if the primary goal of a study is prediction, but essential when the primary goal is describing species-habitat relationships. Pronounced multicollinearity of predictor variables may affect parameter estimation in regression models (Legendre and Legendre 1998). Using these criteria, I eliminated six of the 12 original covariates: dominant tree species, average canopy height, understory volume at two heights, shrub species richness, and average understory height. The final six covariates used in subsequent regression modeling were average dbh, percent canopy closure, tree species richness, tree density, understory density from 0-2 m, and understory density above 2 m.

I further restricted the covariates used in each model set by developing hypotheses about habitat use patterns of each species based on my field observations, and retaining only the covariates in the hypotheses for each species. The same variables were chosen for each species in both dry and rainy seasons; based on field observations I hypothesized that each focus species used the habitat in similar ways across seasons, i.e. a species which is found primarily in the understory in the dry season is also found primarily in the understory in the rainy season.

For the Pink-headed warbler, I hypothesized that tree species richness, percent canopy closure, and understory density from 0-2 m and above 2 m would be important in determining habitat use patterns. This warbler appeared to be highly dependent on dense forest understory for foraging. Not only does the warbler build its nest in grasses below thick understory, but it is also a common member of mixed-species flocks, which are often found moving through the forest canopy in areas with high percent canopy closure. Hypothesizing a positive relationship with both dense understory and closed canopy seems contradictory. However, this forest had a high level of horizontal heterogeneity due to logging and grazing activities. There were many areas in the forest where a 25 m radius circle included an open canopy with dense understory immediately adjacent to a closed canopy with sparse understory. The Pink-headed warbler commonly occurred in this heterogeneous habitat type, and thus I hypothesized a positive relationship with both covariates. Finally, since the warbler was more frequently detected in coniferous forest (lower tree species richness) than in mixed forest (higher tree species richness), I hypothesized a negative relationship with tree species richness.

Like most hummingbirds, the Amethyst-throated hummingbird occurs in areas with open canopy and dense understory, often near banks of flowers on the edge of open areas in the forest. Accordingly, I hypothesized that densities of this hummingbird would be negatively related to percent canopy closure, with a positive relationship with understory density at both the 0-2 m and above 2 m level. I also hypothesized that the Amethyst-throated hummingbird would have a positive relationship with tree species richness, since many of the broad-leaf trees in the forest, especially the Canac *(Chiranthodendron pentadactylon*) have large flowers which I often saw being exploited by hummingbirds.

In the forests of Los Altos, the Rufous-browed wren was detected most often in areas of mature forest which had been logged, where dense understory had grown up to fill the gaps. This species is almost always found on or near the forest floor, where it moves through the understory foraging for insects. For this reason, I hypothesized that density of the wren would be positively related to average diameter at breast height of trees, and positively related to understory density at both the 0-2 m and above 2 m level. In order to produce this uniform understory with little horizontal heterogeneity, the canopy must be relatively open. Accordingly, I hypothesized that wren densities would be negatively related to percent canopy closure. Finally, higher detections of the wren in areas with mixed forest suggested that the wren density is positively related to tree species richness (mixed forests has higher species richness than coniferous forests).

The Brown creeper in Guatemala, like its cousins in North America, is a bark forager which travels through all vertical levels of the forest as it moves upward along the trunks. Therefore, I hypothesized that this species would have a positive relationship with covariates

which measured the density and abundance of trees at a point: tree density and percent canopy closure. Additionally, this species was almost always detected in coniferous forests, and not as often in the mixed forest habitat type. I hypothesized that densities would have a negative relationship with tree species richness (mixed forests have higher species richness than coniferous forests).

The Steller's Jay is primarily a ground forager, and so is more commonly found in or near open areas in the forest; therefore, I hypothesized that Steller's Jay densities would have a negative relationship with percent canopy closure. I also included understory in the model; though I was not sure whether jay densities would have a positive or negative relationship with understory, I concluded that it might be important to a ground forager which is often found in the lower levels of the forest. Since the jay is an omnivore, I hypothesized that its density would be positively related to tree species richness, since more species of trees means more diverse food resources for a bird capable of taking advantage of seeds, berries, fruits, insects, and even other birds which nest in these areas.

I created diagnostic plots to check for non-linear relationships between the response variable (point-level density) and each of the six covariates. I plotted the point -level density for each species, in each season against the reduced set of covariates which I hypothesized would be the most important to that species (total of 80 plots). From this I was able to identify where quadratic terms might improve the fit of the model.

To build, evaluate, and interpret models for species-habitat relationships, I chose to fit all possible models and to use model averaging based on Akaike's Information Criterion corrected for small sample size, rather than use a hypothesis testing framework (Burnham and

Anderson 2002). Information criteria such as AICc work by trading off explained variation in the data against model complexity. This approach has many advantages for analyzing ecological data: it allows the investigator to simultaneously evaluate a whole suite of candidate models, rather than only comparing two models as in inferential statistics, and by way of model-averaging it allows for the ranking of model covariates based on the entire model set (Burnham and Anderson 2002). For my analysis, I used AICc , a modified AIC criteria which is adjusted for small sample size. First, I calculated AICc , delta AICc values, and Akaike weights to determine which models had the most support in the data, and to evaluate the relative importance of the vegetation covariates. Next, I calculated model-averaged regression coefficients for each covariate to quantify the magnitude of their effect on the point level density estimates for each species, in each season.

To determine which models had more support in the data, I fit the full model set for each species and calculated AICc delta AICc values (Δ_i), and Akaike weights (w_i) for each model (Burnham and Anderson 2002). AICc values of each model are relative; they are simply representative of the model's fit to the data relative to the rest of the models. The Δ value of a given model *i* is computed as $AICc_{(i)} - AICc_{(best\ model)}$, so as Δ_I increases, the strength of support for model *i* decreases. Models with AICc within two Δ_I are considered to have approximately equal support in the data. I also computed Akaike weights (w_i), which can be interpreted as the probability that model *i* is the best model in the sample set.

Across all species in both the rainy and dry seasons, the model sets showed considerable uncertainty regarding the best model in the set. All models were within four Δ_I, and Akaike weights (w_i) were distributed fairly evenly across the models. Therefore, I used a

model-averaging approach to estimate weighted regression coefficients; this approach incorporates model selection uncertainty into the process of regression coefficient estimation. Rather than take the β_i estimates from the "top" model, this method makes inference to the entire model set, weighting the regression coefficient estimates from each model by that model's w_i, and then summing across models to obtain a model-averaged β_i estimate. Since my analysis was exploratory, not explanatory, I used the "shrinkage" method; all models were included in the model-averaging, even models in which the β_i being estimated did not appear. This pulls the estimates back down toward zero, and thereby avoids overestimation of the effect size of β_i. I also calculated unconditional 95% confidence intervals for each β_i to determine whether they contained zero (Burnham and Anderson 2002). This modeling process is summarized in Figure 3.

RESULTS

Estimates of detection probability and density

All models were post-stratified by season because distinct differences in behavior and detection probability were noted between seasons. The results of the models (Tables 6 and 7) show that there is a significant difference in detection probability and density from the wet to dry season for some species, but not for others.

Detection probabilities for the Pink-headed warbler were similar across seasons ($\hat{p}_{Dry}$ = 0.1748 (0.139, 0.218); $\hat{p}_{Rainy}$ = 0.2487 (0.198, 0.311)) (Table 6), but estimates of warbler density between seasons differed ($\hat{d}_{Dry}$ = 15.258 ha^{-1}; $\hat{d}_{Rainy}$ = 8.48 ha^{-1}) (Table 7). Similarly, the Rufous-browed wren and the Amethyst-throated hummingbird had comparable detection

probabilities in the rainy and dry seasons (Table 6), but significantly different density estimates between seasons (Table 7).

Detection probabilities for the Steller's Jay (*C. stelleri*) differed between seasons ($\hat{p}_{Dry}$ = 0.9049 (0.776,1.000); $\hat{p}_{Rainy}$ = 0.3123 (0.199,0.489)) (Table 6). However, the density estimates for this species were not significantly different between seasons ($\hat{d}_{Dry}$ = 1.03 ha^{-1}; $\hat{d}_{Rainy}$ = 1.55 ha^{-1}) (Table 7).

The Brown creeper showed no seasonal variation in either detection probability ($\hat{p}_{Dry}$ = 0.3596 (0.283,0.560); $\hat{p}_{Rainy}$ = 0.3981 (0.247,0.523)) (Table 6) or density ($\hat{d}_{Dry}$ = 4.84 ha^{-1}; $\hat{d}_{Rainy}$ = 4.21 ha) (Table 7). Finally, estimates of detection probabilities for the Pooled Trochilidae data set were not significantly different between the rainy and dry seasons ($\hat{p}_{Dry}$ = 0.1237 (0.083, 0.183); $\hat{p}_{Rainy}$ = 0.1819 (0.124, 0.267)) (Table 6). No density estimates were calculated for this dataset because it represents a pooling of multiple species.

Habitat use patterns

One clear pattern across all focus species was that the majority of the models in the full model sets differed very little in terms of model weight; that is, there was not overwhelming support for one "best" model based on Akaike weight. Additionally, most of the models for each species explained minimal amounts of the variance in density among points (r^2 range from 0.039 to 0.223). The relative importance of covariates and the β estimates for meaningful covariates presented below should be interpreted in the context of these overall modeling results.

Covariates included in the full model set for the Pink-headed warbler were tree species richness, canopy closure, understory density 0-2 m, and understory density >2m (full model dry season r^2 = 0.188; full model rainy season r^2 = 0.0856). Of these covariates, cumulative Akaike weights showed that understory density >2m was most important in the dry season ($w_{UD>2}$ = 0.694), and understory density from 0-2 m was most important in the rainy season (w_{UD0-2} = 0.593) (Table 8 and Figure 4). Model-averaging revealed that only two covariates were meaningfully (i.e. confidence intervals did not include zero) related to warbler density: canopy closure (β_{CCDry} = 6.53, (1.08, 11.98)) and understory density >2 m ($\beta_{UD>2Dry}$ = 8.07 (2.39, 13.75))in the dry season, and understory density <2 m in the rainy season ($\beta_{UD<2Rainy}$=4.528 (0.03, 9.03))(Table 8 and Figure 4).

The model set for the Amethyst-throated hummingbird contained the same covariates as the Pink-headed warbler model set, but the results of model-averaging suggests that this species uses the habitat in a different way than the warbler (full model dry season r^2 = 0.223; full model rainy season r^2 = 0.0456). Cumulative Akaike weights showed that tree species richness was the most important covariate for explaining spatial variation in hummingbird densities in the dry and rainy season ($w_{TreeRichDry}$ = 0.686; $w_{TreeRichRainy}$ = 0.686), with canopy closure a distant second (w_{CCDry} = 0.366; $w_{CCRainy}$ = 0.366) (Table 8 and Figure 5). However, model-averaged estimates showed that tree species richness had a meaningful effect only in the rainy season ($\beta_{TreerichRainy}$ = 2.24, (2.12, 2.36)), while canopy closure was meaningful across seasons (β_{CCDry} = 19.91, (13.69, 2.13); $\beta_{CCRainy}$ = -2.20, (-2.49, -1.91), although the change in the sign of β_{CC} suggested that the hummingbird used habitat differently in each season. Understory density

above 2 m was also meaningful across seasons ($\beta_{UD>2Dry}$ = 26.24, (19.70, 32.78); $\beta_{UD>2Rainy}$ = 0.547, (0.248, 0.848)) (Table 8 and Figure 5).

Five covariates were used to model the relationship between habitat and densities of the Rufous-browed wren, and a review of the diagnostic plots justified the addition of a quadratic term for understory density above 2 m (full model dry season r^2 = 0.220; full model rainy season r^2 = 0.206). Here, as with all other models where a quadratic term was justified, the linear term was left in the model. Of these covariates, the most important in the dry season were average dbh ($w_{AvgdbhDry}$ = 0.622) and tree species richness ($w_{TreerichDry}$ = 0.629) closely followed by the quadratic term for understory density above 2 m ($w_{UD>2^2Dry}$ = 0.577) (Table 8 and Figure 6). In the rainy season, tree species richness emerged as the covariate of primary importance ($w_{TreerichRainyy}$ = 0.791), again followed by the quadratic term for understory density above 2 m ($w_{UD>2^2Dry}$ = 0.559). Model-averaged regression coefficients indicated that tree species richness ($\beta_{TreerichDry}$ = 0.96, (0.05, 1.87)), ($\beta_{TreerichRainy}$ = 0.73, (0.63,0.83)); canopy closure (β_{CCDry} = -0.15, (-0.22, -0.08)), ($\beta_{CCRainy}$ = -0.23, (-0.31, -0.15)); and understory density above 2 m ($\beta_{UD>2Dry}$ = 1.99, (1.74, 2.24)), ($\beta_{UD>2Rainy}$ = 0.48 , (0.24, 0.71)); and its quadratic term ($\beta_{UD>2^2Dry}$ = 3.57, (3.33, 3.83)), ($\beta_{UD>2^2Rainy}$ = 1.83, (1.58, 2.08)), were all meaningful predictors of wren density in both seasons (Table 8 and Figure 6).

The three covariates used to model the Brown creeper's habitat use patterns were tree density, tree species richness, and canopy closure, plus a quadratic term for canopy closure in the dry season (full model dry season r^2 = 0.039; full model rainy season r^2 = 0.131). Of these, canopy closure was the most important in both seasons ($w_{CCRainy}$ = 0.893), represented by the quadratic term in the dry season (w_{CC^2Dry} = 0.543) (Table 8 and Figure 7).

The covariates included in the model for Steller's Jay were tree species richness, canopy closure, both understory covariates, and a quadratic term for canopy closure (full model dry season $r^2 = 0.102$; full model rainy season $r^2 = 0.153$). All covariates had equal, low importance in the dry season (Table 8 and Figure 8), but in the rainy season tree species richness was the most important covariate ($w_{TreerichRainy} = 0.879$), closely followed by the quadratic term for canopy closure ($w_{CCRainy} = 0.482$). However, model-averaged regression coefficient estimates were small and not meaningful (Table 8 and Figure 8), with the exception of tree species richness in the rainy season ($\beta_{TreerichRainy} = 1.50$, (0.42, 2.60)).

DISCUSSION

Often researchers conducting studies in tropical areas have limited funding and are only able to spend short amounts of time in their study area. In order to leverage this time and money most effectively to obtaining useful, applicable results, it is essential to have a preliminary understanding of the basic ecology of species of conservation concern. Of the focus species in this study, three are endemic (Pink-headed warbler, Amethyst-throated hummingbird, and Rufous-browed wren) and one of these is threatened (Pink-headed warbler). The results of this analysis provide the first information about detection probabilities, densities, and habitat use patterns of these important species, as well as about the more widespread Brown Creeper and Steller's Jay.

Estimates of detection probability and density

The detection probabilities and density estimates obtained for these species reveal some expected patterns which coincide with the known ecology of the species, as well as several new insights. These new insights will help future researchers refine and adapt their study designs to

the specific challenges of this poorly-studied tropical forest type. In particular, it is clear that detection probability for tropical birds in this region should not be assumed to approach one. Future study designs should incorporate distance sampling or occupancy modeling frameworks in order to calculate detection probabilities and obtain unbiased estimates of density.

The Steller's Jay was the only species which showed a significant difference in detection probability between seasons; in the dry season detection probability approached one, whereas in the rainy season it dropped to 0.31227. Like many jays, this species is very vocal and its calls are distinctive, so the detection probability was expected to approach one. The drop in detection probability in the rainy season suggests that this species is far less vocal during this time, perhaps in an effort to conceal the location of its nest during the breeding season.

For the Pink-headed warbler and the Rufous-browed wren, detection probability was marginally higher in the rainy season than the dry season (Table 6; non-significant difference). I expected this pattern to be more pronounced, since the males of these species have distinctive songs which they sing only during the breeding season, which coincides with the beginning of the rainy season. Higher detection probabilities in the breeding season are a well-known phenomenon in the study of bird populations (Earnst and Heltzel 2002). The hummingbirds and the Brown Creeper also have breeding songs, but they are not as distinctive from their year-round calls as are the breeding songs of the Pink-headed warbler and the Rufous-browed wren, and were not as recognizable to the observer.

The estimates of detection probability for the Pooled Trochilidae dataset did not vary significantly between seasons. This may be because the breeding season in Guatemala for three of the four hummingbird species pooled in this set falls between July and September, months

which were not surveyed during this study (Howell and Webb 1995). Therefore, the vocalizations and behaviors of the hummingbirds would have been fairly uniform throughout the months sampled in this survey (late November 2008-June 2009), with the exception of the Broad-tailed hummingbird, which breeds from April to July in Guatemala and therefore may have shown altered behavior or calls on sampling occasions during this time period. Since hummingbirds are among the most common bird families in the tropics, and information on their distribution and behavior is scarce, it is hoped that this information about hummingbird detection probabilities proves useful for future researchers.

Density estimates were obtained for five species. Three species showed significant differences in density between seasons, even after correcting for seasonal differences in detectability. The Pink-headed warbler, the Amethyst-throated hummingbird, and the Rufous-browed wren all showed significantly higher densities in the dry season than in the rainy season (Table 7). It is interesting to note that these three species are all endemic; the non-endemic Brown creeper and Steller's jay showed no significant difference in densities between seasons.

In the case of the Amethyst-throated hummingbird, where density appears to be more than three times greater in the dry season than in the wet season, this pattern is easily explained. Like many tropical forests in Central America, the forests of Los Altos show strong seasonal patterns in the flowering and fruiting of many plants. The majority of the trees and understory plants in Los Altos flower during the dry season, probably in order to maximize vegetative growth in the wet season and to take advantage of pollinating and dispersing agents in the dry season (Heithaus et al. 1975; Veblen 1978; Lic.P. Pardo, personal communication). This distinct phenology creates an abundance of food in the dry season for nectarivores like the

Amethyst-throated hummingbird. When the dry season passes and many plant species stop flowering, food resources presumably become scarce and the hummingbirds must move to lower elevation areas (Levey and Stiles 1992; Lara 2006). Lara (2006) found a similar pattern in hummingbird habitat use in his study of a comparable high-altitude pine-oak forest in Mexico; in this study, four of seven species in the genus *Lampornis* occurred in the study area, and all were shown to be altitudinal migrants. Further studies are needed to confirm that in Los Altos, as in Lara's study area, the Amethyst-throated and other species of hummingbirds migrate altitudinally in response to seasonal changes in the distribution of available nectar from flowering plants. If this is the case, then hummingbird conservation depends on conservation of lower-altitude habitat surrounding Los Altos. This is challenging since the majority of forest habitat adjacent to the park is small patches isolated in cultivated fields; in most cases it is only a matter of time before these patches are razed to plant more crops.

Like the Amethyst-throated hummingbird, the Pink-headed warbler and the Rufous-browed wren appear to be resident, but not necessarily stationary. Spatial and temporal variation in resources necessitates seasonal movements on local scales. This may be especially true for these three species, because they are largely dependent on the understory layer of the forest, where resources may fluctuate more rapidly than in the canopy. Although the understory is not fully deciduous, it becomes dry and ceases to flower by the end of the dry season, and is also more frequently impacted by grazing and fires than the canopy (personal observation). Therefore, these understory-dependent birds may show significant variation in local densities as they move over an area of the forest larger than my 200 ha study area in pursuit of resources.

A second possible explanation for the variation in densities of warblers and wrens between seasons is that in the dry season the lower-altitude agricultural lands which surround the forest become arid and barren as crops dry up and are burned in preparation for the next year's planting. Therefore, these birds would probably move away from understory near the forest edge and become more densely concentrated in the interior forest, where many plants are flowering during the dry season and the insect population is correspondingly high. In the rainy season, crops begin to grow in the fields and it becomes more feasible to forage in understory along the forest edge and even to use crop fields as a corridor to move to other forest patches in search of food. This would result in higher observed densities of warblers and wrens in my study area in the dry season.

Even considering these possible effects of season on local densities of these three species, the density estimate for the Pink-headed warbler in the dry season was extremely high (estimated density = 15.258/hectare) (Table 7). Previous researchers in the tropics have observed that density estimates in these ecosystems are often affected by the low vocalization rates of many tropical birds. This leads to violations of the distance-sampling assumption that the detection probability at the point is one (Gale et al. 2009). However, in this study, species with sufficient detections were also among the most mobile and vocal, and so under-estimation of abundance probably did not occur. On the contrary, the Pink-headed warblers in particular were so active that in some cases individuals may have actually been double-counted, leading to an over-estimation of abundance.

Like most sampling methods, distance sampling has strict assumptions. The most important assumption is that all objects at the sample point are detected with a probability of

one (this is expressed as g(0) = 1). Violation of this assumption leads to negatively biased density estimates. Other assumptions of distance sampling are that all objects are detected at their initial location (i.e. no movement of animals as a response to observer) and that all distance measurements are exact (Buckland et al. 2001; Buckland et al. 2004). During data collection, there was no evidence that the assumptions of g(0) = 1 or of exact measurements were violated. However, birds did display "flushing" behaviors in response to observers moving into an area, and I often saw this happen at my points. This violates the assumption that birds were detected at their initial location. After analyzing the data in DISTANCE 6.0, I was able to diagnose this problem and account for it by forcing the distance bins near zero, i.e. creating a bin that contains all detections from zero to the distance of the first detections. This correction minimized the possibility of underestimating species densities.

Habitat use patterns

Few previous studies have evaluated the relationships between bird species and habitat in tropical ecosystems similar to those of Los Altos (Eisermann and Schultz 2005; Lara 2006; Renner et al. 2006; Rotenberg 2007). Rather than focus on individual species, these studies identified general patterns of community abundance and diversity in different types of habitat, e.g., logged versus undisturbed forest. While these community-level indices are essential for conservation, it is also important to recognize that not all species in a community use habitat in the same way, and that habitat use may vary by season. The results of this study provide important insights into patterns of habitat use in a set of focus species which appear to differentially use habitat within and among seasons.

Results indicate that densities of the Pink-headed warbler, the Amethyst-throated hummingbird, and the Rufous-browed wren were all positively related to understory density. The Pink-headed warbler appeared to use understory differently between seasons: in the dry season, the warbler foraged at upper levels of the understory and in the canopy, often moving in mixed-species flocks. As expected, the understory density above 2 m and canopy closure were both relatively important predictors of point-level density of the warbler in the dry season. During the wet season when breeding occurs, the warbler builds its nest below dense understory (Griscom 1957). Accordingly, understory density from 0-2 m emerged as the most relatively important and the only meaningful covariate in the rainy season.

In addition to dense understory, the Amethyst-throated hummingbird used areas of the forest with high tree species richness, high canopy closure in the dry season, and low canopy closure in the rainy season. Use of areas with high tree species richness may be a result of the fact that the broad-leaf trees in this forest have flowers which are frequently surrounded by up to three hummingbirds per flower, whereas the coniferous forests provide no nectar resource. Although these trees mainly flower in the dry season, Amethyst-throated hummingbirds maintained foraging "traplines" in the forest and stuck to them year-round. As a result, the birds showed site fidelity even in the rainy season when fewer trees are flowering (Lara 2006).

For the Rufous-browed wren, high tree species richness and dense understory above 2 m emerged as the most important factors of habitat use. These results document higher use of open areas in mixed broadleaf-coniferous forest than of dense, homogenous conifer patches. Similar to other members of the family Troglodytes, the Rufous-browed wren utilized the understory for foraging, cover, and nesting sites. For the wren, as for the Pink-headed warbler

and the Amethyst-throated hummingbird, a dense understory layer of foliage appears to be associated with high local densities of these species. Mangers should note that allowing excessive grazing in the forest, which destroys the understory layer, will probably render such areas unsuitable for these species.

My results indicate that Brown creeper densities were positively associated with high canopy closure and high tree density. High levels for these covariates describe a dense, mature forest, which would provide the creeper with a larger surface area of bark from which to glean insects. For the Stellar's Jay, densities were negatively associated with canopy closure (both seasons) and understory density above 2 m (dry season), perhaps because the jay is a ground forager and prefers open areas with very little understory.

With few exceptions, many of the habitat covariates were not meaningfully related to densities of the focus species at the point level. This is probably due to the fact that, as in most observational studies of wildlife, not all factors influencing a system can be controlled or measured. In choosing covariates, I attempted to select characteristics that measure key compositional and structural components of the habitat and factors found important in previous bird-habitat studies. However, it is clear from the r^2 values of my models (0.039 to 0.223) that much of the spatial variability of the system was explained by unmeasured habitat covariates or by non-habitat factors.

Overall, species-habitat relationships were not as pronounced in the rainy season as in the dry season (i.e. fewer significant regression coefficients, smaller effect size). This may be due to the fact that only half the number of point surveys was made during the rainy season as during the dry season; with only two surveys in the rainy season, the sample size may not have

been large enough to effectively reveal species-habitat relationships. Future studies should address the concerns outlined here by choosing covariates that more fully characterize both understory and canopy attributes and by ensuring adequate sample sizes in each season.

In this study, I had multiple reasons for choosing to work with birds. In addition to the environmental education and income generation opportunities provided by working with highly valued species, birds are also of high ecological importance. Recent research has found that birds exhibit the most diverse range of ecological functions among vertebrates. Two of the most important and well-known functions of birds in ecosystems are as seed dispersers and as pollinators (Sekercioglu 2006). In tropical forests like the forests of Totonicapán, where the majority of mammals have been extirpated through hunting, birds are one of the only remaining seed dispersers. In addition, tropical forest understory herbs, such as those which make up the understory of the Totonicapán forests, are known to rely heavily on pollination by birds (Sekercioglu 2006). Consequently, understanding and protecting the avifauna of these threatened forests is of the utmost importance.

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CHAPTER 3: CONSERVATION OF THE BIRD COMMUNITY OF LOS ALTOS IN A COMMUNAL MANAGEMENT CONTEXT: CHALLENGES AND SOLUTIONS

INTRODUCTION

The goal of the Peace Corps Masters International (PCMI) program is to provide an integrated, applied education to graduate students willing to accept the challenges and reap the rewards of international research work. As part of the program, students are required to coordinate their education between their university of choice and their Peace Corps service. Students complete one to two years of coursework at their university, then accept a Peace Corps assignment and spend 27 months living and working in their host country. During this time, students must fulfill all the requirements of a Peace Corps volunteer, including learning to work in a new language and culture, attending conferences, meetings, and trainings to improve their capabilities as a volunteer, and identifying community needs and developing projects to meet those needs. The PCMI program provides host communities with a more highly trained, specialized, and knowledgeable volunteer, and provides the volunteer with a unique, practical education which extends far beyond the scope of most traditional Master's programs.

I was a student in the PCMI program from 2005-2010 in the Department of Fish, Wildlife, and Conservation Biology at Colorado State University and in my Peace Corps site of Totonicapán, Guatemala. During my time as a Peace Corps volunteer, I focused on community

conservation projects and worked to tie these projects into my Master's research on the bird community of the regional park Los Altos de Totonicapán. In this chapter, I detail some of the challenges and rewards of these collaborative conservation projects.

Objectives

The objectives of this chapter are 1) to provide a political and cultural context for the research described in the first two chapters of this thesis and 2) to report on a series of conservation projects I conducted in tandem with my research on the bird communities of Los Altos, in fulfillment of the Peace Corps portion of my PCMI degree. These projects were designed to further conservation of the forests of Los Altos and the birds which inhabit them, within the complex political landscape of Totonicapán.

GOVERNANCE OF LOS ALTOS

The city of Totonicapán lies in the western highlands of Guatemala, in a large valley east of Quetzaltenango, the country's second largest city after Guatemala City. This valley is bordered to the east by the extinct volcano Cuxlikel (3100 m elevation), to the west by the summit of Campanabaj (3300 m elevation) and to the north and south by rolling, forested mountain ranges. Totonicapán has the highest percentage of indigenous people of any department in the country; of the 110,000 inhabitants, barely 7 percent register themselves as "ladino" (INE 2000). Most local people claim that the town is actually 99 percent indigenous. The indigenous culture of Totonicapán is Maya K'iche, and the majority of the town's citizens speaks and/or understands K'iche. Unlike in many rural areas of Guatemala, almost everyone in the city and surrounding villages also speaks Spanish.

A unique characteristic of Totonicapán is its well-established and powerful system of community organization. Many towns and cities in the highlands have some form of community organization which operates parallel to the municipal government, but in the case of Totonicapán this community organization is so powerful and influential that it has earned Totonicapán the reputation, both locally and internationally, of being an almost wholly indigenously governed, semi-autonomous political entity (Conz 2008). The center of this organization is the Alcaldes Comunales de los 48 Cantones (Mayan Mayors Council). The Mayan Mayors Council is an adapted form of political organization from the colonial era; it consists of 48 elected mayors, one from each village surrounding the city, each charged with the administration of his respective village (Conz 2008). Today, the Council represents the highest Mayan authority in the city. Mayors are elected by their community and serve for a period of one year without compensation. The service is known as the "kax kol", or burden of honor; if they do not choose to accept the unpaid "honor", they may find their house set on fire or their water cut off by angry neighbors. The Council's principal responsibilities include registering births and deaths, overseeing the general order of village life, settling land disputes, and acting as intermediary between the municipal government and the village. It has the power and support base in the communities to call protests that shut down principal national highways at an hour's notice, to mete out extrajudicial "Mayan punishments", and to challenge the municipal government on almost any issue, including ownership of the communal forests.

CONSERVATION CHALLENGES

Los Altos: The communal forests

In addition to community organization, Totonicapán is famous for the extensive coniferous forests that blanket the mountains bordering the city and belong collectively to its residents. These forests are the best-conserved coniferous forests remaining in the country, and encompass 16,400 hectares, extending from the southern border with the department of Solola to the edge of the city itself (between coordinates 14º 49´/91º 11´ and 14º 56´/ 91º 19). The dominant tree species in the forest are white pine (*P. ayacahuite),* Colorado pine *(P. rudis),* Cypress (*C. lusitanica),* Sauco (*Sauco mexicanus),* various oak species (*Quercus spp.)*, and the most southern-growing fir in the world, the Pinabete (*Abies guatemalensis*). As a result of its unique combination of climate and altitude and its relative isolation as an ecosystem, the forest harbors a high level of endemism among its flora and fauna. At least 10 endemic mammals are documented, including Goodwin's small-eared shrew (*Cryptotis goodwini*), six species of mouse (*Microtus guatemalensis, Habromys lophurus, Scotinomys teguina, Reithrodontomys sumichrasti, Peromyscus aztecus* and *P. levipes*), a squirrel (*Sciurus aureogaster*), and Gray's long-tongued bat (*Glossophaga leachii*). As described in Chapter 1 of this thesis, 94 different species of birds have been identified in the forests, including 29 regional endemics.

These forests have belonged to the people of Totonicapán for thousands of years (Veblen 1977; Conz 2008). Long before the Spanish conquistador Pedro de Alvarado arrived with his conquering armies in the 1524, Maya K'iché people used the forests surrounding their city for firewood, pasture, building materials, and other extractive purposes (Veblen 1977). Under Spanish colonial rule, unoccupied lands were no longer considered to be communal, but

rather were property of the Spanish crown, and ownership of these lands could be transferred to interested parties (Ekern 2006). In this way, large areas of the communal forests were granted to Spanish nobles as "encomiendas" (parcels). The 16,400 hectare tract which comprises the modern-day communal forests was originally the encomienda granted to the local representative of the Spanish government in Totonicapán, and it was this representative's responsibility to administer and control local use of the encomienda (Conz 2008). The Spanish government also oversaw the establishment of the Mayan Mayors Council, which they viewed as an efficient method of monitoring and reporting on activities in the rural hamlets surrounding the main city of Totonicapán (Conz 2008). Another primary duty of the Council was to manage and protect the communal forests of the encomienda.

When Spanish confirmed the Mayan Mayors Council as the primary governing body for the indigenous population of Totonicapán, they simultaneously established the "municipio", or state-sanctioned municipal government, as the parallel government for citizens of Spanish descent: this is known as the "Two Republic" system (Wittman and Geisler 2005). By the 18th century, the Two Republic system was ubiquitous throughout Guatemala, and the municipal governments continuously tried to erode their indigenous counterpart's rights to land and resources (Wittman and Geisler 2005). In the western highlands, local indigenous leaders upheld their authority to a greater extent than communities elsewhere in Guatemala. For example, in Totonicapán the Mayan Mayors Council was able to retain authority over the city's communal forests, despite the municipal government's best efforts to claim the forests for themselves (Conz 2008).

When Guatemala gained its independence from Spain in 1821, the municipal governments sold vast tracts of communal lands throughout the highlands region to an emerging, powerful class of coffee growers. Situated at altitudes too high for profitable coffee production, the great forests of Totonicapán were unattractive for external buyers, and thus the forest remained under the administration of the Mayan Mayors Council. Demarcation of core areas of the forest and additional land acquisitions were carried out by the Council during this time (Ekern 2006).

In 1997, international NGOs and the municipal government established a cooperative agreement whereby the communal forests of Totonicapán were declared a regional-municipal park within the Guatemalan National Park Service (CONAP). The park, named Los Altos de Totonicapán, encompasses 16,400 has of the highest altitude forest above the city, and roughly corresponds with the previously established boundaries of the communal forest (Albacete and Espinoza 2002). This agreement was possible without the participation or agreement of the Mayan Mayors Council because two titles to the forest exist: one original, post-independence title held by the Council and one more recent, state-sanctioned title held by the municipal government (Ekern 2006). Regardless of the fact that Los Altos is now part of the national system of protected areas administered by CONAP, and that the "official" title is held by the municipal government, practical use and management of the forest continues to be controlled by the Mayan Mayors Council.

Efforts by the municipal government and the state to control ownership and management of Los Altos may ultimately be deleterious to long-term forest health. Various studies examining links between land tenure and conservation have shown that lands occupied

and managed by the original indigenous communities are better conserved and more productive than those managed by a distant central government (Katz 2000, Larson 2003, Wittman and Geisler 2005, Bray et al. 2008). In western Guatemala, Secaira (2000) found a significant difference in forest cover in areas owned by indigenous communities (42% forest cover) as compared to areas owned by the state or private citizens (32% forest cover). Similarly, an earlier study found that 57% of the department of Totonicapán remained forested as of 1992, when the national average of forest cover was only 30% (Wittman and Geisler 2005).

Degradation of the forest

Despite Totonicapán's conservation triumphs relative to the rest of Guatemala, in the decade since the communal forest was declared a regional park several factors have combined to cause considerable ecosystem degradation. The principal factor is increased pressures on the forest from a continually growing human population. Although the forest provided firewood, water, and construction materials for a resident population of more than 100,000 Maya K'iché in the years before the Spanish conquest, the current population of Totonicapán is more than 350,000 people, and the population growth rate exceeds 2 percent (Veblen 1977; CIA World Fact Book, 2009). This population growth has two effects: first, there is an increased local demand for firewood, water, construction materials, and other extractive forest products, and second, more and more citizens of Totonicapán find themselves without traditional means of subsistence, which is defined by enough land to grow sufficient corn and beans to feed their family. In the face of abject poverty, many people turn to the forest for survival, illegally cutting communal trees for personal profit. Alternatively, many men immigrate illegally to the United States in search of higher wages and a chance to lift their family out of poverty. However, these

emigrants actually exacerbate pressures on Los Altos. Realizing they may be caught and deported from the U.S. at any moment, many of these men send money back to Totonicapán and direct their families to purchase the keys to a more sustained prosperity: chainsaws and dumptrucks. With this equipment replacing their handsaws and donkeys, local families are able to exploit the forest at an unprecedented rate, sometimes illegally clear-cutting multiple acres of the forest in a single day. Although this behavior is denounced by the community and by the Council, there are often multiple families involved and multiple bribes passing to Council members, and so action is not always taken to stop these depredations.

CONSERVATION SOLUTIONS

The challenges faced by the community of Totonicapán as they struggle to integrate cultural influences from the United States with traditional forest management approaches are enormous. However, there are always solutions. As a Peace Corps Volunteer, I was in a unique position to create conservation solutions which tailored first-world perspectives and techniques to the conservation needs of this distinctive communally-managed forest.

The agency which hosted me during my 30 months in Totonicapán is Asociación CDRO (Cooperativo para el Desarollo Rural Occidente), an NGO founded in 1988 by local community leaders. Within CDRO, I was assigned to work directly with environmental programs. I worked mainly with the small park, Sendero Ecológico El Aprisco, which was run by CDRO as an experiment in local environmental education. The park lies 5.5km to the west of the city, on the edge of Los Altos, and is composed of 13has of coniferous forest and open meadows, and a central area with cabins, offices, and a large classroom. I was initially based out of this park, but

eventually branched out to initiate projects with other local organizations, including the Mayan Mayors Council.

Environmental education

The public schools of Totonicapán do not have a mandatory environmental education component of their curriculum. Any efforts at environmental education are conducted largely by the MARN (Ministry of the Environment) and non-profits like CDRO. These organizations realize that in order to guarantee a safe future for the forests of Los Altos, the people of Totonicapán must understand, identify with, and recognize the value of these forests: environmental education of both adults and children plays an essential role in achieving this goal.

As described above, the central mission of Sendero Ecologico El Aprisco is to provide environmental education opportunities to local people. To this end, the park is equipped with an indoor classroom, a small biological library, and two full time employees whose purpose is to teach visitors about the forests of Los Altos and about ecology and conservation in general. During my time at the park, I carried out several projects to enhance the environmental education program in El Aprisco. I collected more than 50 new books, magazines, and education videos, all in Spanish, for the park's library. I coordinated with the two environmental educators to improve and expand the content of their lesson plans, and to introduce novel teaching methods like "interactive learning" where visitors participate in a environmentally-themed game and then discuss what they learned. In collaboration with other park staff, I designed and installed a 2km interpretive trail in the park to enhance visitor appreciation of the forest. The

trail has 10 stopping points, with a fiberglass sign at each point explaining an aspect of forest ecology relevant to that point on the trail.

In addition to these internal projects, I also developed a number of projects which allowed El Aprisco to share its expertise in environmental education with the larger community of Totonicapán. These projects were beneficial for the environment and helped to improve park-community relations. In 2007, my co-workers and I approached the director of the elementary school in the village adjacent to El Aprisco with a plan to help the school incorporate environmental education into their curriculum. Together with the director and the school's teachers, we identified the most urgent environmental issue in the village as waste management, and designed a lesson plan to teach classes focused on this topic. For the entire school year, my co-workers and I visited the school once a week and taught a tailored, interactive class to each grade in the school. As a final event, the students helped organize a community beautification project. The students collected more than eight pickup truckloads of garbage from community roadways, streams, and forest areas, and presented their accomplishments to their parents at a closing celebration. In 2008, we extended this program to the local high school, and designed and taught a year of classes focused on the ecology of the communal forests of Los Altos.

Finally, we completed one environmental education project at the scale of the entire municipal government of Totonicapán. In 2007, we organized an art competition to educate students, teachers, and families about the plight of the endangered fir in Los Altos, the Pinabete (*Abies guatemalensis*). Although the Pinabete once blanketed the mountains of Los Altos, it is now endangered due to high demand for its branches and for young trees as Christmas

decorations (Andersen et al. 2008). Impoverished locals know the Pinabete is disappearing, but as long as they can make a small profit selling the branches to wealthy city dwellers, they will continue to harvest it unsustainably. In El Aprisco, we held a competition in which local school children would compete for the best "Save the Pinabete" poster design. Sixteen schools participated, and in each of these schools we gave a seminar on the Pinabete's ecology and status. Of the 250 entries in the poster contest, the top three winners received a free family pass to El Aprisco. Their posters were printed and distributed around Totonicapán and neighboring Quetzaltenango to increase awareness of the Pinabete's plight, which we hoped would cause a decrease in demand.

Environmental Education Materials

As I spent more time in Totonicapán, I learned more about the city's unique political system and began to realize the importance of coordinating conservation projects with the Mayan Mayors Council. To gain permission from this group to conduct my thesis research in Los Altos, I had to propose a tangible product to deliver in return for their support. After many meetings with the Council president and many presentations before the entire Council, we agreed to co-produce two environmental education tools which would help promote conservation of birds in Los Altos, and also increase the Council's reputation for productivity in the community. The first of these tools was a complete guide to the birds of Totonicapán (Appendix 2). This guide includes a photograph of each of the 94 species of birds identified during my thesis research, with the Spanish, English, Latin, and Maya K'iché name next to a description of the species' habitat and diet. Cover art was created by a local artist, and more than 20 local farmers attended a meeting to identify the Maya K'iché names of each bird.

Money to print the guide was jointly raised between CDRO and the Peace Corps, and 500 copies were printed in 2009. Copies were distributed to all of the agencies which co-manage the forest, and were used in environmental education workshops; they are currently for sale at the Mayan Mayors Council offices and at El Aprisco. This booklet is the first guide to the birds of Totonicapán ever produced, and was received with great excitement in the community.

The second environmental education material I produced in collaboration with the Mayan Mayors Council was a set of posters featuring the endemic birds of the communal forest of Los Altos. The motivation for this project was the fact that most local people, especially students, could not afford the bird guide. The Council proposed the creation of an alternative educational material which would serve the same purpose, but would be affordable and therefore more likely to be used in the schools. Most elementary and high school students in Totonicapán cannot afford textbooks. Instead, local bookstores offer students "laminas", single glossy sheets with summary information on topics ranging from Greek history to calculus. We decided to create a set of three small laminated posters, about the endemic birds of Totonicapán, so that students would have access to information about the biodiversity of their communal forests. Working together, we designed three posters featuring 27 of the 29 regionally endemic bird species; each bird is described by a large photo, Spanish and Latin names, and a brief, fun life history fact. The Mayan Mayors Council raised more than $1,500 from the development organization Ecologic to print 6,000 copies of the posters. To promote the use of the posters in the curriculum of the city' schools, we organized and carried out two "Teaching Biodiversity" workshops with more than 100 teachers. In these workshops, the project's field technicians, the forestry technician from the Council, and I taught the teachers

about the bird diversity of the communal forests and about how their students can help protect that diversity. Currently, the posters are for sale in the Mayan Mayors Council offices and in two of the largest bookstores in town; profits are invested in the Council's tree nursery in Los Altos. As of November 2009, the posters had sold out and the Council was raising funds to print a second batch.

Alternative Income Generation

The guide to the birds of Totonicapán and the endemic bird posters served a dual purpose: to provide educational materials to help local people learn about and value their forest resources, and to generate much-needed income for the Mayan Mayors Council. Income generation projects are a centerpiece of many conservation efforts in Latin America, and the Peace Corps has encouraged volunteers to initiate this type of project. I helped to develop an alternative income generation with El Aprisco and the neighboring forest parcel.

While conducting my thesis research, I invited many Guatemalan and international ornithologists to visit El Aprisco and help me learn about the unique avian community of the adjacent forests of Los Altos. These experts agreed that the avifauna of the area was unique and accessible, and that potential for an eco-tourism project focused on bird watching was high. My co-workers and I in El Aprisco began thinking about how to make such a project work: El Aprisco was only 13 hectares, with at least five hectares devoted to soccer fields, parking lots, and buildings, and therefore did not offer extensive hiking or bird watching possibilities. We decided to propose a partnership to the neighboring "Parcialidad Tax", a forest parcel which encompassed more than 200 hectares of conifer and mixed forest, sprinkled with cold waterfalls and deep green caves. This forest parcel was communally owned and managed by the Tax clan,

a local family group with more than 200 members. The terms of the proposed ecotourism partnership project we proposed were that El Aprisco would market the project and host the visitors, while the Parcialidad Tax would allow access to their forest and provide young people to serve as guides. To prepare the young people for this position, El Aprisco organized, recruited for, and carried out a six week guide training course. Twelve young people from the Parcialidad participated in the course, which covered topics including conservation of natural resources biology of the birds of Totonicapán, basic legislation governing tourism in Guatemala, customer service, leadership, first aid, and basic English. Upon completion of the course, the guides were ready to lead groups of national and international tourists on hikes in the Parcialidad, and were also new conservation leaders in their communities. As of March 2010, five of the twelve guides are still regularly employed in the project.

Conservation planning support

One of the benefits to a host community of having a PCMI volunteer is that he or she may have training and experience which other non-Masters volunteers may not. In my case, my coursework at CSU provided me with a wide range of skills, including knowledge of ArcGIS software and understanding of basic ecological principles which I was able to apply to two final projects. The first of these projects was a mapping project coordinated with the Mayan Mayors Council. Until this project, the Council monitored and controlled the boundaries of Los Altos without the use of maps. Each November, the entire community of Totonicapán, e.g., the formal owners of the communal forests of Los Altos, gathered in town and embarked on a three-day hike around the boundary of the forest. The purpose of this traditional trek is to reestablish the boundaries of the communal forest and to ensure that the majority of the

community agrees on the location and status of these boundaries. While this is an extremely effective method of communal forest management, it does not equip the Council with legally recognized tools for asserting their ownership of the forest in the face of pressure from the municipal government and CONAP, who do not always recognize communal ownership of Los Altos. Throughout Latin America, this problem of indigenous populations lacking the skills and knowledge to create precise, defensible maps of their lands is a common paradigm (Davis and Wali 1994).

In the spring of 2008, the Council asked if I could help them obtain mapping software and train them to use it, so they could map the forests of Los Altos for both management and litigation purposes. I worked with the forestry technician (the Council's only non-voluntary, permanent position) to write a grant to a firm called GEOSISTEC, which donates ArcGIS software to rural municipalities in Guatemala. We were able to convince GEOSISTEC that the Council deserved ArcGIS as much as any municipal government, and in October of 2008 the software, valued at $5,000, was installed in the Council's offices. Over the next three months, I taught weekly classes in basic ArcGIS to the Council forestry technician, two interested Mayors, and four forestry technicians from the municipal Forestry Office. On the annual hike that November, we used two borrowed GPS units to mark coordinates for the forest boundaries, and used ArcGIS to create the first formal map of the community-sanctioned boundaries of the forests of Los Altos. The Council is currently using ArcGIS to map the locations of the more than 1,200 springs in the communal forest.

I was also able to offer conservation planning support to the managers of the Parcialidad Tax. The board of directors of the Parcialidad came to El Aprisco in 2007 with a

request for a scientific assessment of their forest parcel. They were contemplating entering into a contract with the Guatemalan Forest Service, INAB, to harvest lumber from the Parcialidad, but did not trust INAB to fairly assess the condition and value of their forest. Co-workers and I designed a simple study by using a grid to place 25 random circular plots of radius 13 m (approximately ½ hectare) in the Parcialidad, in which we measured average dbh, tree density, canopy height, canopy closure, shrub diversity, understory height, and which species of trees were present. We also recorded any wildlife encountered during these visits. This information was synthesized into a professional report and delivered to the board of directors of the Parcialidad in February of 2008. The board presented the report to their more than 200 members, many of whom were very interested in the species lists and later became involved in our project to create the guide to the birds of Totonicapán and in the tourism guide training course.

FUTURE DIRECTIONS

It is my hope that the projects I completed during my time in Totonicapán contributed to the conservation of the forests of Los Altos and of the birds which inhabit them. Since many of these projects were coordinated with local counterparts, they should be sustainable in the long-term. It is worth noting that perhaps the majority of these projects would probably never have been initiated nor successfully carried out were it not for my own and other volunteers' drive, passion, expertise, and access to outside sources of information and funding. Unlike many regions of Guatemala, Totonicapán has few foreign NGOs and their associated volunteers; this means that sustainable projects must be truly, internally, sustainable, and not simply passed on from one NGO to the next.

Based on my time in the forests of Los Altos and with the people of Totonicapán, I have faith that this unique, important ecosystem can successfully be preserved through the community's centuries-old traditional management system. For this to happen, the people of Totonicapán and the outsiders who wish to help them must learn to have patience, understanding, and flexibility as they struggle to integrate Western influences into their culture, while preserving their reverence for the forest that gave this region its first name: K'iché, land of many trees.

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TABLES

Table 1: Abbreviations of original habitat covariates

Covariate	**Abbreviation**
Average canopy height	Avg C
Average undersstory height	Avg U
Canopy closure	CC
Average diameter at breast height	Avg dbh
Dominant tree species	DT spp.
Elevation	Elev
Shrub species richness	S rich
Tree density	Tree D
Tree species richness	Tree rich
Understory density <0.3m	UD<0.3m
Understory density 0.3-1m	UD0.3-1m
Understory density 1-2m	UD1-2m
Understory density 2-3m	UD2-3m
Understory density 0-2m	UD0-2m
Understory density >2m	UD>2m

Table 2: Correlation matrix of habitat covariates

Cross correlations between the 13 original covariates; each pair of covariates with a correlation coefficient of >0.60 with one other covariate (vertical lines) and/or >0.40 with more than one other covariate (stippled) were eliminated, except for the understory covariates, which were combined into two new derived covariates (Understory density 0-2 m and Understory density >2 m).

	Avg C	Avg U	CC	Avg dbh	DT spp.	Elev	S rich	Tree D	Tree rich	UD<0.3m	UD0.3-1m	UD1-2m	UD2-3m
Avg C	1.000	0.016	0.453	**0.696**	-0.228	-0.454	-0.036	-0.115	-0.186	0.109	0.194	0.073	-0.017
Avg U	0.016	1.000	0.116	0.091	-0.287	0.105	**0.705**	-0.394	-0.078	0.371	0.481	0.485	**0.695**
CC	0.453	0.116	1.000	0.366	**-0.562**	**-0.613**	0.203	0.423	-0.075	0.050	0.225	0.080	-0.020
Avg dbh	**0.696**	0.091	0.366	1.000	-0.223	-0.364	0.095	-0.165	-0.384	0.200	0.260	0.297	0.046
DT spp.	-0.228	-0.287	**-0.562**	-0.223	1.000	0.283	-0.200	0.016	0.450	0.046	-0.173	-0.081	-0.106
Elev	-0.454	0.105	**-0.613**	-0.364	0.283	1.000	0.077	-0.373	0.054	0.080	-0.061	0.040	0.206
S rich	-0.036	**0.705**	0.203	0.095	-0.200	0.077	1.000	-0.219	0.132	0.457	**0.569**	**0.545**	**0.528**
Tree D	-0.115	-0.394	0.423	-0.165	0.016	-0.373	-0.219	1.000	0.373	-0.292	-0.100	-0.157	-0.368
Tree rich	-0.186	-0.078	-0.075	-0.384	0.450	0.054	0.132	0.373	1.000	0.289	0.252	0.193	0.108
UD<0.3m	0.109	0.371	0.050	0.200	0.046	0.080	0.457	-0.292	0.289	1.000	**0.765**	**0.567**	**0.584**
UD.3-1m	0.194	0.481	0.225	0.260	-0.173	-0.061	**0.569**	-0.100	0.252	**0.765**	1.000	**0.854**	**0.664**
UD1-2m	0.073	0.485	0.080	0.297	-0.081	0.040	**0.545**	-0.157	0.193	**0.567**	**0.854**	1.000	**0.725**
UD2-3m	-0.017	**0.695**	-0.020	0.046	-0.106	0.206	**0.528**	-0.368	0.108	**0.584**	**0.664**	**0.725**	1.000

Table 3: Estimates of measures of variation in species richness between seasons

Seasonal estimates of avian species richness, proportions of shared species, number of species present in one season but not the other, and average species detection probability in the study area in Los Altos.

Quantity ($\widehat{\theta}$)	Estimator	$\widehat{\theta}$	$\widehat{SE}$ ($\widehat{\theta}$)	Lower 95%	Upper 95%
Number of species present in Rainy which were observed in Dry	$\widehat{N}$	37.34	3.11	32.00	44.50
Number of species present in Dry which were observed in Rainy	$\widehat{N}$	37.25	3.12	27.48	39.50
Proportion of Dry species still present in Rainy	$\widehat{\varphi}$	0.83	0.07	0.70	0.98
Proportion of Rainy species present in Dry	$\widehat{\varphi}$	0.93	0.08	0.69	1.00
Colonizing species: number of species not present in Dry, but present in Rainy	$\widehat{\lambda}$	3.14	3.12	0.00	10.62
Species detection probability in Dry	$\hat{p}$	0.93	0.05	0.81	1.00
Species detection probability in Rainy	$\hat{p}$	0.92	0.04	0.83	1.00

Table 4: Structure coefficients for variables and canonical correlations and redundancy coefficients for canonical variates for both seasons

Dry season: Structure coefficients for habitat and species variables

	Canonical variate			
Variable	**1**	**2**	**3**	**4**
Tree species richness	-0.1363	-0.3866	-0.1636	0.8973
Average dbh	-0.8388	0.0677	0.2462	-0.4809
Canopy closure	-0.3339	0.6089	0.6742	0.2513
Understory density	-0.5054	0.5497	-0.6279	0.2195
Brown creeper	-0.0012	0.3493	0.5479	-0.3532
Steller's Jay	0.4029	0.3057	-0.0250	-0.0126
Pink-headed warbler	-0.3182	0.3389	0.3626	0.4623
White-eared hummingbird	-0.7367	0.1666	-0.3190	-0.4830
Amethyst-throated hummingbird	-0.4816	0.4323	-0.0881	0.3033
Rufous-browed wren	-0.6533	-0.3660	-0.0059	-0.0783
Rufous-collared robin	-0.3920	-0.2351	0.5767	-0.4208

Dry season: Canonical correlations and redundancy coefficients

Canonical variate	Canonical correlation	Redundancy coefficient
1	0.8777	0.1781
2	0.6709	0.0472
3	0.5722	0.0409
4	0.3617	0.0158

Rainy season: Structure coefficients for habitat and species variables

	Canonical variate			
Variable	**1**	**2**	**3**	**4**
Tree species richness	0.6650	-0.1924	-0.5603	0.4547
Average dbh	-0.3141	-0.5095	-0.1514	-0.7866
Canopy closure	-0.6878	-0.6269	-0.2537	0.2637
Understory density	0.3744	-0.8030	0.4629	0.0261
Brown creeper	-0.3718	-0.2284	0.1690	0.3400
Steller's Jay	0.4960	-0.0388	0.3934	0.4051
Pink-headed warbler	-0.1392	-0.6086	0.6523	-0.3038
White-eared hummingbird	0.4509	0.7171	0.1890	-0.2596
Amethyst-throated hummingbird	0.5487	-0.3865	-0.4329	-0.4433
Rufous-browed wren	0.5192	-0.4136	-0.2799	0.3462
Rufous-collared robin	-0.4182	-0.1267	-0.1575	-0.3008

Rainy season: Canonical correlations and redundancy coefficients

Canonical variate	Canonical correlation	Redundancy coefficient
1	0.7552	0.1102
2	0.5959	0.0647
3	0.3155	0.0133
4	0.1258	0.0019

Table 5: Tests of dimensionality for the canonical correlation analysis in the dry and rainy season

Dry Season

Canonical variate	WilksLamda	F	df1	df2	p
1	0.07383	3.18744	28	85.10847	0.00002
2	0.32144	1.87321	18	69.21947	0.03312
3	0.58461	1.53791	10	50.87337	0.15338
4	0.86916	0.97847	4	26.00000	0.43633

Rainy Season

Canonical variate	WilksLamda	F	df1	df2	p
1	0.24554	1.43398	28	85.10847	0.10570
2	0.57149	0.83094	18	69.21947	0.65872
3	0.88620	0.31158	10	50.87337	0.97473
4	0.98417	0.10455	4	26.00000	0.97990

Table 6: Dry and rainy season estimates of detection probability

Percent CVs and 95% confidence intervals for bird species with > 60 total detections and > 30 detections in each season (n = 34 points).

Species	Season	$\hat{p}$	%CV	Lower 95%	Upper 95%
Pink-headed warbler	Dry	0.1748	11.3	0.1397	0.2187
Ergaticus versicolor	Rainy	0.2487	11.33	0.1985	0.3115
Amethyst-throated Hummingbird *Lampornis amethystinus*	Dry	0.1281	17.07	0.0916	0.179
	Rainy	0.1239	16.82	0.0884	0.1739
Rufous-browed wren	Dry	0.3952	16.45	0.2849	0.5479
Troglodytes rufociliatus	Rainy	0.5214	10.11	0.4254	0.6391
Brown creeper	Dry	0.3981	17.15	0.283	0.56
Certhia americana	Rainy	0.3596	18.74	0.2472	0.523
Steller's Jay	Dry	0.9049	7.62	0.7769	1
Cyanocitta stelleri	Rainy	0.3123	22.22	0.1992	0.4896
Pooled Trochilidae	Dry	0.1237	20.07	0.8342	0.1835
	Rainy	0.1819	18.96	0.124	0.267

Table7: Dry and rainy season density estimates per hectare

Percent CVs and 95% confidence intervals for bird species with > 60 total detections and > 30 detections in each season (n = 34 points). Density estimates were not calculated for Pooled Trochilidae.

Species	Season	$\hat{d}$	%CV	Lower 95%	Upper 95%	SE
Pink-headed warbler	Dry	15.258	11.35	12.185	19.105	1.73
Ergaticus versicolor	Rainy	8.481	11.63	6.732	10.684	0.98
Amethyst-throated Hummingbird *Lampornis amethystinus*	Dry	11.622	17.07	8.314	16.247	1.98
	Rainy	3.086	16.83	2.199	4.331	0.52
Rufous-browed wren	Dry	4.466	16.5	3.218	6.198	0.73
Troglodytes rufociliatus	Rainy	2.442	10.32	1.985	3.003	0.25
Brown creeper	Dry	4.843	17.2	3.44	6.819	0.584
Certhia Americana	Rainy	4.213	18.86	2.801	6.141	0.795
Steller's Jay	Dry	1.033	7.62	0.887	1.203	0.795
Cyanocitta stelleri	Rainy	1.551	22.24	0.989	2.431	0.344

Table 8: Summary table of results of species-habitat modeling hypotheses and results

Species	Hypotheses	Relatively important predictors (predictors with w_i >0.40)		β estimates and 95% C.I.s for meaningful predictors			
		Dry	Rainy	Dry	95% C.I.	Rainy	95% C.I.
Pink-headed warbler	(-) Tree rich						
	(+) CC	w_i = 0.629		β_{CC} = 6.53	(1.08, 11.98)		
	(+) UD 0-2m		w_i = 0.593			$\beta_{UD<2}$ = 4.528	(0.03, 9.03)
	(+) UD >2m	w_i = 0.694	w_i = 0.473	$\beta_{UD>2}$ = 8.07	(2.39, 13.75)		
Amethyst-throated hummingbird	(+) Tree rich	w_i = 0.686	w_i = 0.686			$\beta_{Treerich}$ = 2.24	(2.12, 2.36)
	(-) CC			β_{CC} = 19.91	(13.69, 2.13)	β_{CC} = -2.20	(-2.49, -1.91)
	(+) UD 0-2m					$\beta_{UD<2}$ = 0.932	(0.724, 1.140)
	(+) UD >2m			$\beta_{UD>2}$ = 26.24	(19.70, 32.78)	$\beta_{UD>2}$ = 0.55	(0.25, 0.85)
Rufous-browed wren	(+) AvgDBH	w_i = 0.622		B_{DBH} = 0.08	(0.06, 0.09)		
	(+) Tree rich	w_i = 0.629	w_i = 0.791	$\beta_{Treerich}$ = 0.96	(0.05, 1.87)	$\beta_{Treerich}$ = 0.73	(0.63, 0.83)
	(-) CC			β_{CC} = -0.15	(-0.22, -0.08)	β_{CC} = -0.23	(-0.31, -0.15)
	(+) UD 0-2m						

Species	Hypotheses	Relatively important predictors and model weights (w_i >0.40)		β estimates and 95% C.I.s for meaningful predictors			
		Dry	Rainy	Dry	95% C.I.	Rainy	95% C.I.
Rufous-browed wren	(+) UD >2m	w_i = 0.474	w_i = 0.414	$\beta_{UD>2}$ = 1.99	(1.74, 2.24)	$\beta_{UD>2}$ = 0.48	(0.24, 0.71)
	(+) UD>2^2	w_i = 0.577	w_i = 0.599	$\beta_{UD>2^2}$ = 3.57	(3.33, 3.83)	$\beta_{UD>2^2}$ = 1.83	(1.58, 2.08)
Brown Creeper	(+) Tree den		w_i = 0.583				
	(-) Tree rich						
	(+) CC	w_i = 0.409	w_i = 0.893			β_{CC} = 4.84	(3.84, 4.99)
	(+) CC^2	w_i = 0.543					
Steller's Jay	(+) Tree rich		w_i = 0.879			$\beta_{Treerich}$ = 1.50	0.42, 2.60
	(-) CC						
	(-) CC^2		w_i = 0.482				
	(-or +) UD 0-2m						
	(-or +) UD >2m						

FIGURES

Figure 1: Reference maps of Guatemala and the study area

The map on the right is a reference map indicating where in Guatemala the forests of Los Altos de Totonicapán are located. The map on the left represents the ~200ha study area, on the western edge of Los Altos, with points indicated by circles.

Figure 2: COMDYN estimates for global species richness in the dry and rainy season

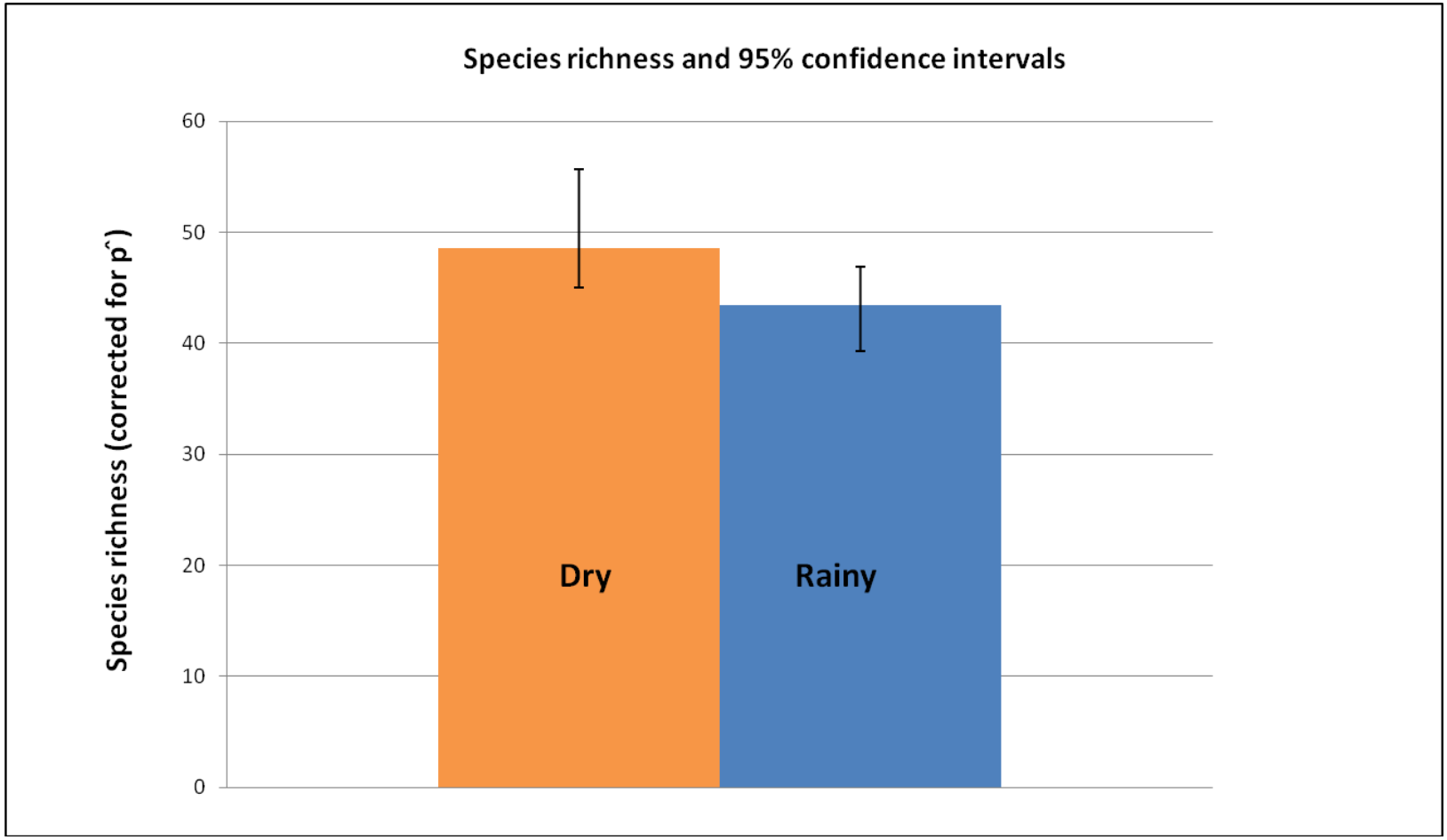


Figure 3: Process for species-level analyses

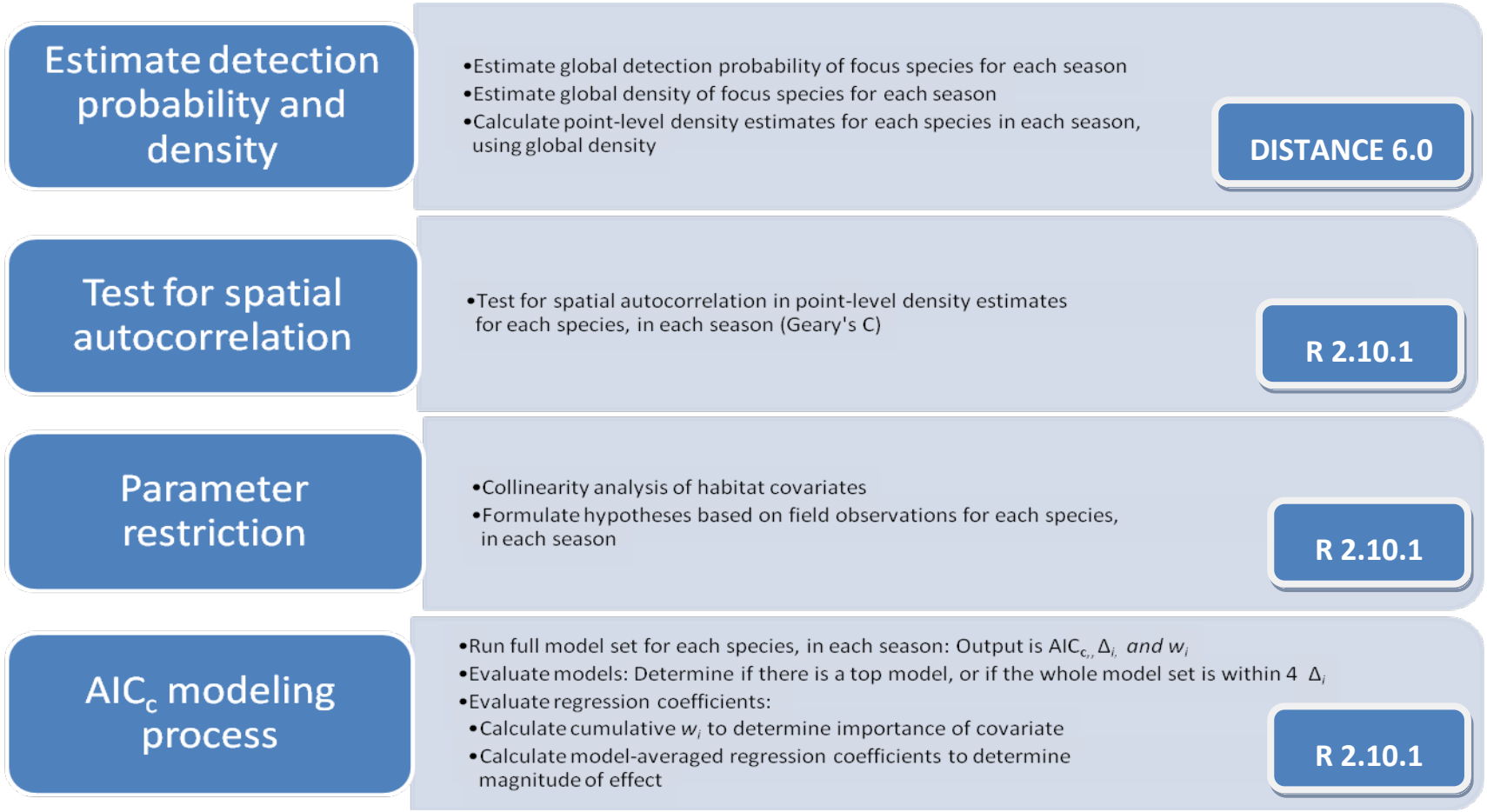


Figure 4: Relative importance of covariates based on cumulative Akaike weights (top graphs) and model-averaged estimates of β coefficients with 95% confidence intervals (bottom graphs) for the Pink-headed warbler.

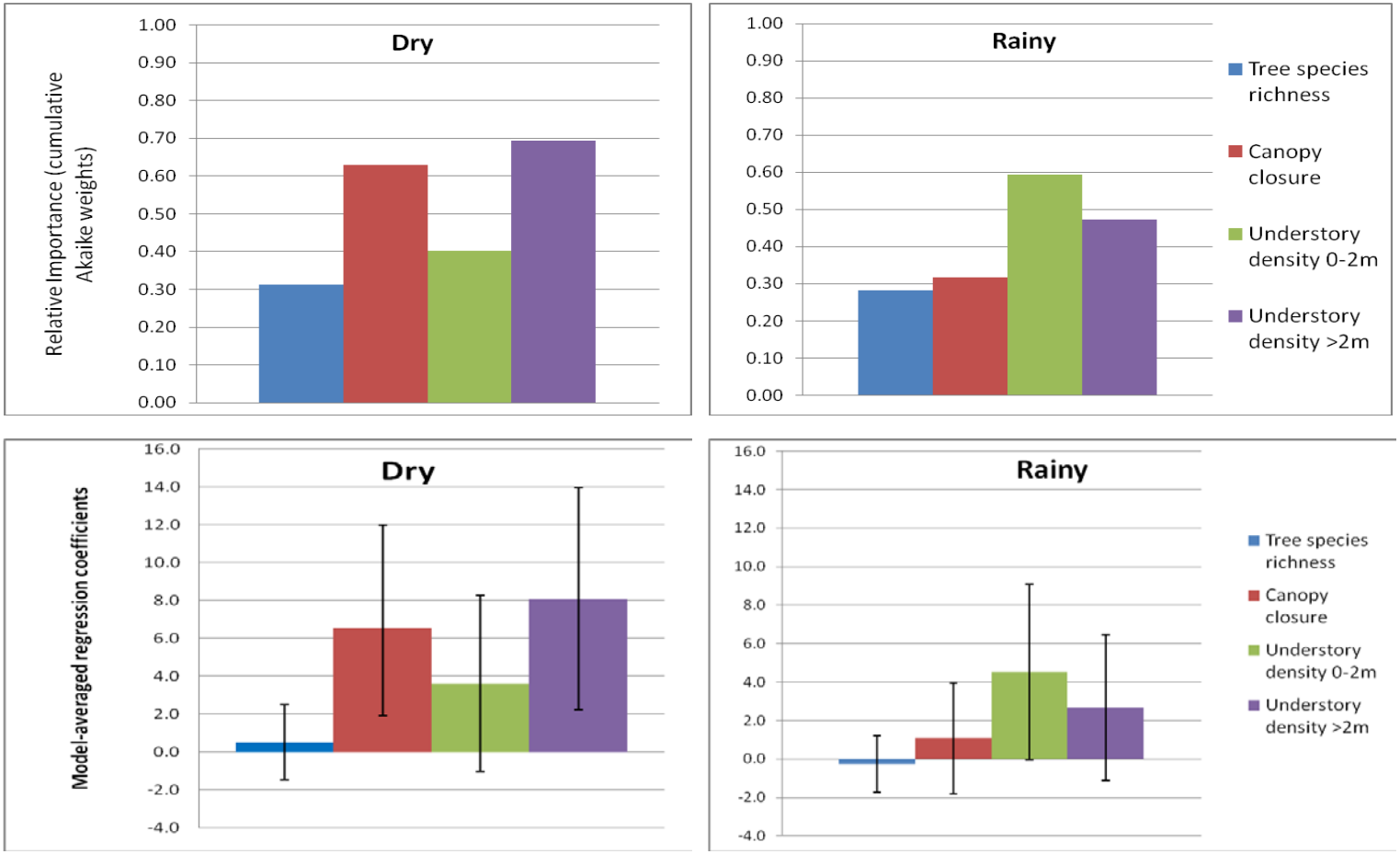


Figure 5: Relative importance of covariates based on cumulative Akaike weights (top graphs) and model-averaged estimates of β coefficients with 95% confidence intervals (bottom graphs) for the Amethyst-throated hummingbird

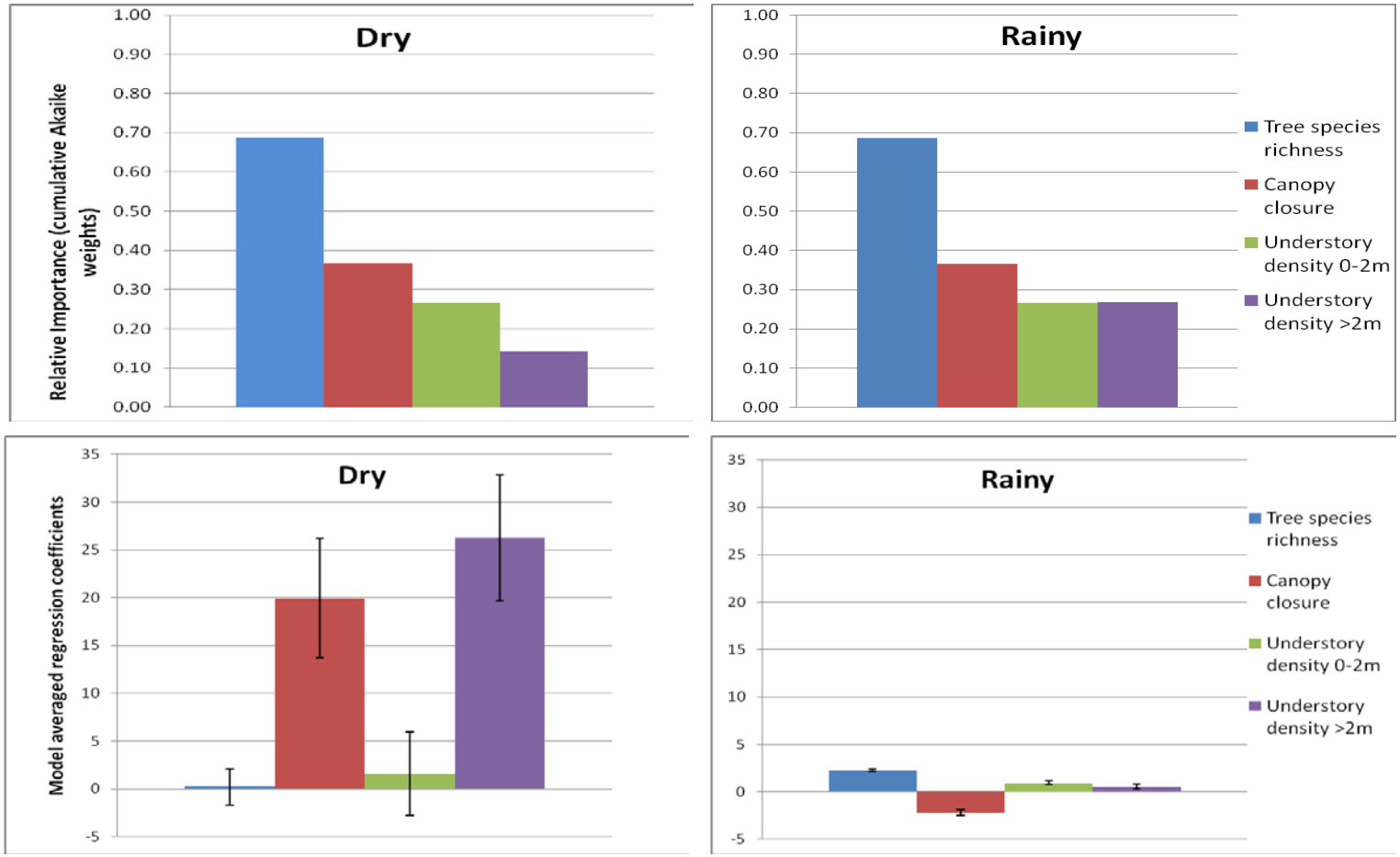


Figure 6: Relative importance of covariates based on cumulative Akaike weights (top graphs) and model-averaged estimates of β coefficients with 95% confidence intervals (bottom graphs) for the Rufous-browed wren.

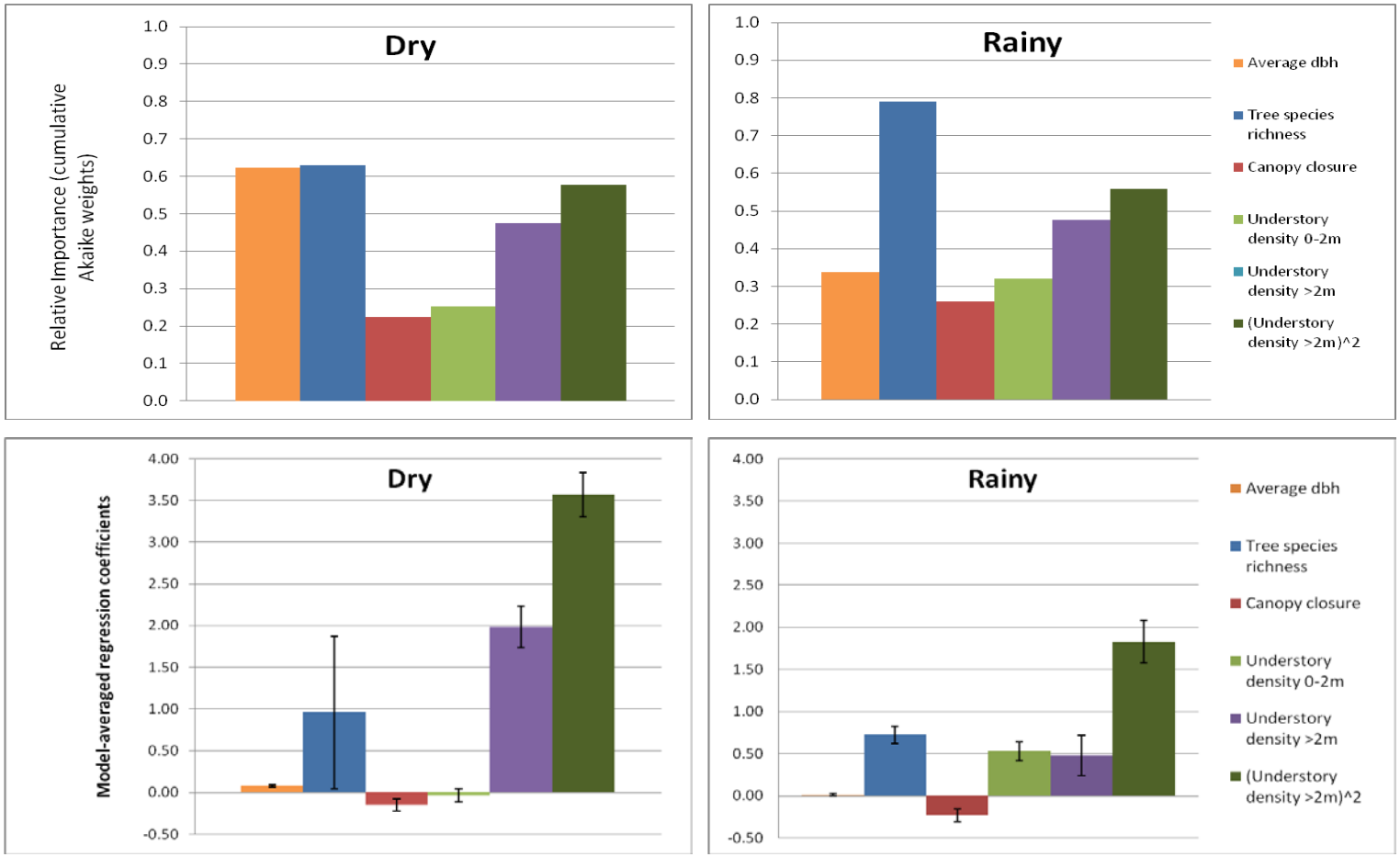


Figure 7: Relative importance of covariates based on cumulative Akaike weights (top graphs) and model-averaged estimates of β coefficients with 95% confidence intervals (bottom graphs) for the Brown Creeper. Note that the quadratic term (Canopy closure^2) is only used in dry season models

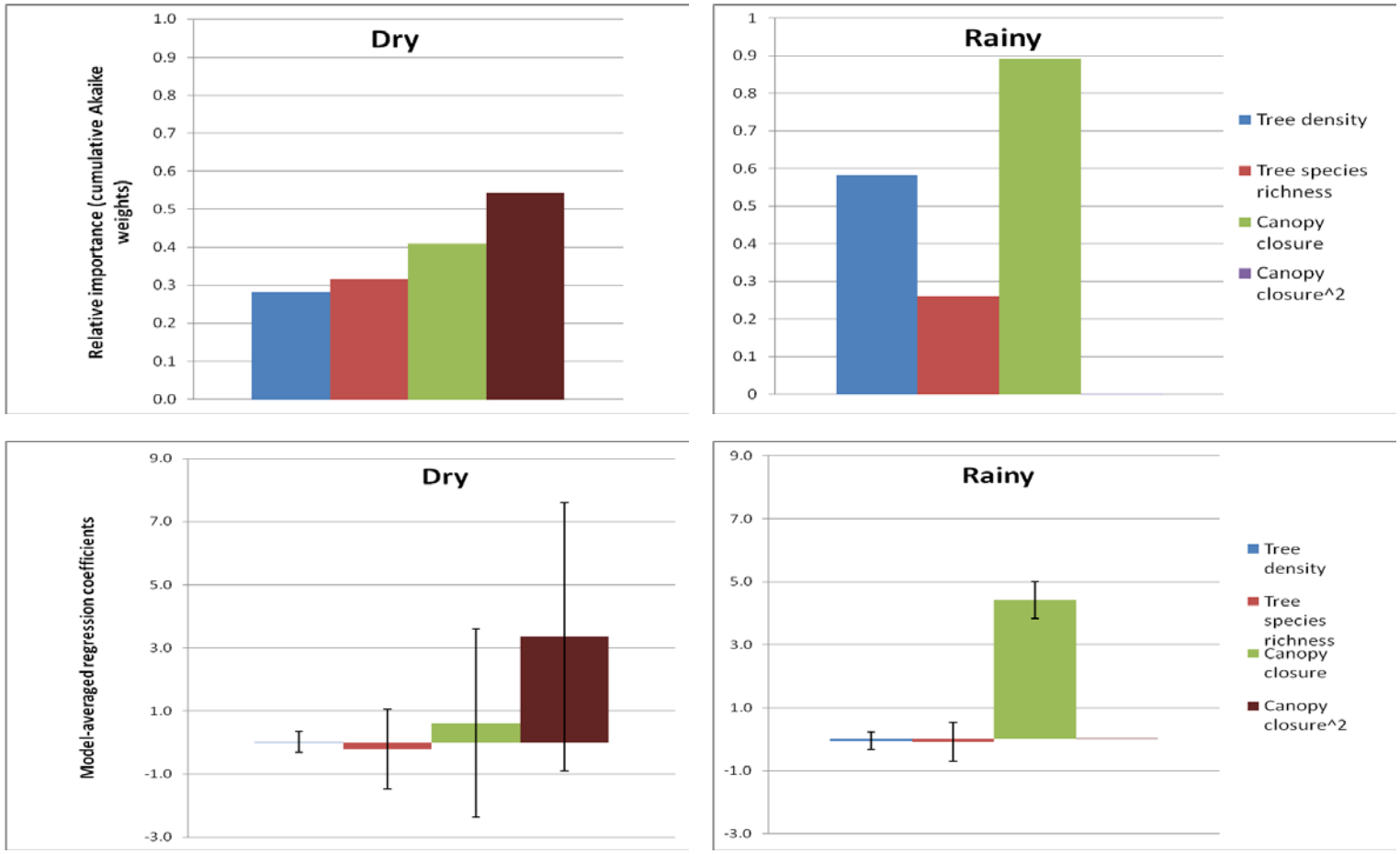
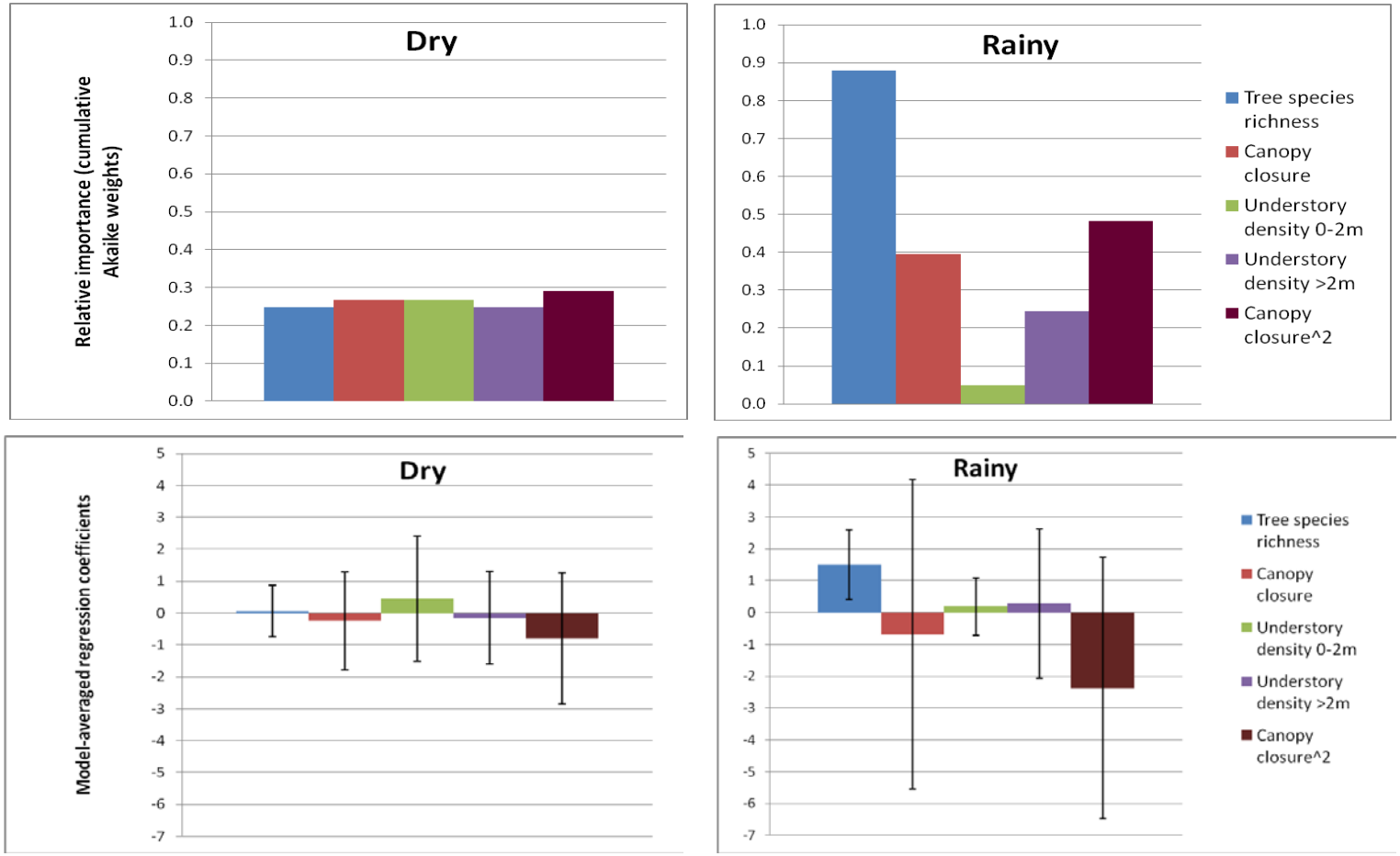


Figure 8: Relative importance of covariates based on cumulative Akaike weights (top graphs) and model-averaged estimates of β coefficients with 95% confidence intervals (bottom graphs) for the Steller's Jay.



APPENDICES

Appendix 1: Species list for Los Altos de Totonicapán

This list contains all bird species identified in Los Altos de Totonicapán from April 2007-June 2009, primarily by Kate Cleary but also by visiting ornithologists including Knut Eisermann, Claudia Avendano, Alvaro Jaramillo, Claire Dallies de Masaya, Samuel Hansson, and Hugo Harold Enriquez. Species are listed alphabetically (not in taxonomic order) by family.

Common Name	***Scientific Name***	**Family**	**Migrant/ Resident**
Red-tailed hawk	*Buteo jamaicensis*	Accipitridae	R
Bushtit	*Psaltriparus minimus personatus*	Aegithalidae	R
Chesnut-collared swift	*Cypseloides rutilus griseifrons*	Apodidae	R
Vaux's swift	*Chaetura vauxi*	Apodidae	R
White-collared swift	*Streptoprocne zonaris mexicanus*	Apodidae	R
White-throated swift	*Aeronautes saxatalis*	Apodidae	R
Black Vulture	*Coragyps atratus*	Cathartidae	R
Turkey Vulture	*Cathartes a. aura*	Cathartidae	R
Brown Creeper	*Certhia americana*	Certhidae	R
Band-tailed pidgeon	*Columba fasciata*	Columbidae	R
White-tipped dove	*Leptotila verreauxi fulviventris*	Columbidae	R
White-winged dove	*Zenaida asiatica*	Columbidae	R
Northern (common) raven	*Corvus corax*	Corvidae	R

Stellar's Jay	*Cyanocitta stelleri coronata*	Corvidae	R
Unicolored jay	*Aphelecoma unicolor*	Corvidae	R
Lesser roadrunner	*Geococcyx velox melanchima*	Cuculidae	R
Spot-crowned woodcreeper	*Lepidocolaptes affinis*	Dendrocolaptidae	R
Chesnut-capped brush finch	*Atalepes brunneinucha*	Emberizinae	R
Cinnamon-bellied Flowerpiercer	*Diglossa baritula montana*	Emberizinae	R
Rufous-collared sparrow	*Zonotrichia capensis septentrionalis*	Emberizinae	R
Spotted towhee	*Pipilo e. macronyx*	Emberizinae	R
Yellow-eyed junco	*Junco phaeonotus*	Emberizinae	R
Yellow-throated brush finch	*Atlapetes gutteralis*	Emberizinae	R
Scaled antpitta	*Grallaria guatimalensis*	Formicariidae	R
Black-capped siskin	*Carduelis atriceps*	Fringillidae	R
Black-headed siskin	*Carduelis notata forreri*	Fringillidae	R
Hooded grosbeak	*Coccothraustes abeilliei*	Fringillidae	R
Red Crossbill	*Loxia curvirostra*	Fringillidae	R
Black-capped swallow	*Notiochelidon pileata*	Hirundinidae	R
Northern rough-winged swallow	*Stelgidopteryx serripennis*	Hirundinidae	R
Balitimore Oriole	*Icterus galbula*	Icteridae	M
Bronzed cowbird	*Molothrus aeneus*	Icteridae	R

Bullock's Oriole	*Icterus bullocki*	Icteridae	M
Great-tailed grackle	*Quiscalus mexicanus*	Icteridae	R
Blue-and-white mockingbird	*Melanotis hypoleucus*	Mimidae	R
Blue-throated motmot	*Aspatha gularis*	Motmotidae	R
Black and white warbler	*Mnilotilta varia*	Parulinae	M
Crescent-chested warbler	*Vermivora superciliosa*	Parulinae	R
Golden-browed warbler	*Basileuterus belli*	Parulinae	R
Hermit Warbler	*Dendroica occidentalis*	Parulinae	M
Olive warbler	*Peucedramus taeniatus giraudi*	Parulinae	R
Painted Redstart	*Myioborus pictus*	Parulinae	R
Pink Headed Warbler	*Ergaticus versicolor*	Parulinae	R
Slate-throated redstart	*Myoborus miniatus*	Parulinae	R
Tennessee warbler	*Vermivora peregrina*	Parulinae	M
Townsend's Warbler	*Dendroica townsendi*	Parulinae	M
Wilson's Warbler	*Wilsonia pusilla*	Parulinae	M
Yellow-rumped warbler	*Dendroica coronata*	Parulinae	R
House sparrow	*Passer d. domesticus*	Passeridae	R
Occelated Quail	*Cyrtonyx montezumae o C. ocellatus*	Phasianidae	R
Singing Quail	*Dactylortyx thoracicus*	Phasianidae	R

Acorn Woodpecker	*Melanerpes formicivorus*	Picidae	R
Guatemalan Flicker	*Colaptes auratus mexicanus*	Picidae	R
Hairy woodpecker	*Picoides villosus*	Picidae	R
Grey Silky	*Ptilogonys c. cinereus*	Ptilogonatidae	R
Emerald toucanet	*Aulacorhynchus prasinus*	Ramphastidae	R
Great Horned Owl	*Buho virginius*	Strigidae	R
Mountain Pygmy Owl	*Glaucidium gnoma*	Strigidae	R
Whiskered Screech owl	*Otus trichopsis*	Strigidae	R
Golden-crowned kinglet	*Regulus satrapa*	Sylviidae	R
Common Bush Tanager	*Chlorospingus ophthalmicus*	Thraupidae	R
Flame-colored tanager	*Piranga bidentata sanguinolenta*	Thraupidae	R
Hepatic tanager	*Piranga flava*	Thraupidae	R
Western Tanager	*Piranga ludoviciana*	Thraupidae	M
Blue-hooded euphonia	*Euphonia elegantissima*	Thraupinae	R
Amethyst-throated hummingbird	*Lampornis amethystinus*	Trochilidae	R
Azure-crowned hummingbird	*Amazilia cyanocephala*	Trochilidae	R
Broad-tailed hummingbird	*Selasphorus platycerus*	Trochilidae	R
Garnet-throated hummingbird	*Lamprolaima r. rhami*	Trochilidae	R
Green violet-ear	*Colibri thalassinus*	Trochilidae	R

Green-throated mountain gem	*Lampornis viridipallens*	Trochilidae	R
Magnificent Hummingbird	*Eugenes fulgens*	Trochilidae	R
Sparkling-tailed woodstar	*Philodice dupontii*	Trochilidae	R
White-eared hummingbird	*Basilinna leucotis*	Trochilidae	R
Band-backed wren	*Campylorhynchus zonatus restrictus*	Troglodytidae	R
Rufous-browed wren	*Troglodytes rufociliatus*	Troglodytidae	R
Mountain Trogon	*Trogon mexicanus*	Trogonidae	R
Black Robin	*Turdus infuscatus*	Turdidae	R
Brown –backed Solitaire	*Myadestes occidentalis*	Turdidae	R
Eastern bluebird	*Sialia sialis*	Turdidae	R
Hermit Thrush	*Catharus guttatus*	Turdidae	M
Mountain Robin	*Turdus plebejus*	Turdidae	R
Ruddy-capped nightingale thrush	*Catharus frantzii alticola*	Turdidae	R
Rufous Collared Robin	*Turdus rufitorques*	Turdidae	R
Greater Pewee	*Contopus pertinax*	Tyrannidae	R
Hammond's Flycatcher	*Empidonax hammondii*	Tyrannidae	M
Olive -sided Flycatcher	*Contopus borealis*	Tyrannidae	M
Pine Flycatcher	*Empidonax affinis*	Tyrannidae	R
Tufted Flycatcher	*Mitrephanes p. phaeocercus*	Tyrannidae	R

Western Peewee	*Contopus sordidulus*	Tyrannidae	M
Yellowish flycatcher	*Empidonax flavescens*	Tyrannidae	R
Barn Owl	*Tyto alba*	Tytonidae	R
Blue-headed (solitary) vireo	*Vireo s. solitarius*	Vireonidae	M
Hutton's Vireo	*Vireo huttoni mexicanus*	Virionidae	R

Appendix 2: Poster Set: "Las Aves Endémicas de Totonicapán"

This set of posters was created in cooperation with the local Maya K'iché authorities, as part of an environmental education packet or local schools.

Appendix 3: Bird guide for the forests of Totonicapán

This comprehensive bird guide was created in cooperation with the ecological park Sendero Ecologico El Aprisco.